HERBIVORE-MEDIATED EFFECTS ON ECOSYSTEM PROCESSES IN A NEAR-ARCTIC SALT MARSH

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ABSTRACT

Herbivores influence, and often regulate nutrient and energy flow. I investigated interactions between herbivory and the foods on which geese rely while nesting and rearing their broods on the Yukon-Kuskokwim Delta in southwestern Alaska. In a captive Cackling Canada gosling (*Branta canadensis minima*) experiment I decoupled the effects of seasonal declines in forage quality and availability on gosling development. An 11% decline in forage quality translated to goslings that were structurally smaller and 100 g lighter at 31 days of age. Forage availability had similar effects on gosling size, and the combined magnitude of these effects are similar to those observed in wild populations.

I manipulated within-season grazing history of *Carex subspathacea* swards within brood-rearing areas used by Black Brant geese (*Branta bernicla nigricans*). Spatial variation in forage quality and availability exceeded seasonal variation. Brant consumed over 95% of the annual aboveground production of these swards without any short- or apparent long-term effects on aboveground growth.

Adding grazing pressure to *C. ramenskii*, or removing grazing pressure from *C. subspathacea*, resulted in a bi-directional shift in the morphology and nutritional characteristics of these sedges. The areal extent of *C. subspathacea* increased from 2 to 8% of the Tutakoke landscape with a concomitant decrease in *C. ramenskii* meadows between 1991-1998. Brant have been increasing the carrying capacity of the Tutakoke River colony following a population decline in the early 1980's. The population has increased beginning in 1988, yet remains below historic numbers. Density-dependent

effects on gosling growth accompanied the population increase initially. However, gosling mass has increased over the past decade due to herbivore-mediated increases in the areal extent of grazing lawns.

I experimentally flooded the dominant plant communities in the Tutakoke colony with tidal waters in the field. I detected a decrease in standing crop biomass in a community when soil salinity was increased six-fold, but not three times ambient soil salinity. I detected no effect of tidal flooding on soil carbon and nitrogen mineralization rates or soil oxidation-reduction potentials. Plant communities and soil processes are resistant to the effects of tidal inundation at these levels in the Tutakoke River landscape.

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PREFACE

The four chapters in this thesis were written and formatted for separate journals. Chapter 1 was written for publication in the *Auk*, chapter 2 had been published in the *Journal of Ecology* at the time this thesis was completed, chapter 3 was in review at *Oecologia*, and finally chapter 4 was written to meet the specifications for publication in *EcoScience*. I am the first author on these chapters and was primarily responsible for designing the experiments, writing, data analysis, and did the majority of lab and field work. However, my co-authors offered valuable contributions to this work. Roger Ruess at the University of Alaska Fairbanks (UAF), Christopher Babcock (UAF), Jim Sedinger at the University of Nevada (formerly UAF), Mark Herzog (UAF), and R. Michael Anthony at the U. S. Geological Survey, Biological Resources Division (USGS, BRD) provided assistance with ideas, editing, and data collection. Thus, the word 'we' in these chapters refers to the substantial input provided by my co-authors, but I take sole responsibility for any errors herein.

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provided valuable insight, editing, and humor that helped me to appreciate my experience as a graduate student at UAF. Many graduate students have helped me to clarify ideas, and offered stimulating conversations; I thank them. In particular, Chris Babcock helped build my cabin and fixed Isabelle; helped me grow as a scientist, and is a close friend. Amy Zacheis and Kate Doran read drafts of manuscripts and offered me their friendship at a time of my life when it was most needed and appreciated. Bill O'Connell, Jason Schamber, and Mark Herzog made field seasons seem too short and helped me to build my cabin. Other friends in Fairbanks helped make it my home; Joe and Helena Rueter and their son Gabe are among the dearest of them. Connie and Tony Vargas opened their home and hearts to me and I thank them. Finally, I thank my mom Colleen for the many phone calls, care packages and encouragement throughout this work, my brother Marty for his support, and my dad Richard who installed a love for 'da woods' in me when I was young; I wish he had been alive to have shared my experiences as a graduate student.

INTRODUCTION

Movement patterns of herbivores correspond with selection for habitats where efficient use of high quality forage is possible. On a regional scale these movements are principally driven by a coupling of soil fertility, vegetation composition and phenology, and disturbances such as fire (Hobbs and Spowart 1984, McNaughton 1983, 1985, Sedinger and Raveling 1986, Hobbs et al. 1991, McNaughton et al. 1997, Pastor et al. 1997). Habitat selection at the local scale is influenced by landscape topography and snow cover (Nellemann 1994), plant phenology (Fox et al. 1991), forage patch size and architecture (DeToit et al. 1990, Shipley and Spalinger 1995), predation risk and social groups (Scott et al. 1996), and inter- and intraspecific interactions among herbivores (Coppock et al. 1983a, Tardiff and Stanford 1998, van der Wal et al. 1998).

Herbivores face unique nutritional stresses because vegetation tissues are low in dietary protein relative to a diet that incorporates animal tissues, and they have evolved wide variations in body and digestive designs to accommodate this stress (Demment and VanSoest 1985, Hofmann 1989, Robbins 1993, Sedinger 1997). One of the most energetically and nutritionally demanding periods of a herbivore life cycle is during neonate development (Robbins 1993). Herbivores attempt to meet these nutritional requirements by timing their migration patterns and breeding cycles around this critical period of their life cycle, by increasing forage intake rates, and by foraging selectively on plants and plant parts high in nutrients relative to their dietary needs (Sedinger 1984, Klien 1990). Movement patterns of herbivores are perhaps more finely tuned at higher

latitudes because the breeding and post-breeding season is compressed by a short growing season. Vegetation quality is high immediately after green-up but rapidly declines because photosynthetic demands for nitrogen exceed those of leaf elongation throughout the season (Chapin et al. 1980). Herbivores that opportunistically track vegetation green-up benefit from this flush of high quality forage and growth rates of young born early in the season exceed that of those born later (Sedinger and Flint 1991). This can have large impacts on animal life histories and population dynamics (Cooch et al. 1991, Sedinger et al. 1995).

Herbivory influences forage quality and availability through changes in plant growth, community composition, and rates and pathways of nutrient cycling (Coppock et al. 1983b, Bazely 1986, Ruess et al. 1989, Hik and Jefferies 1990, Pastor and Naiman 1992, Mulder and Ruess 1998). Thus, feedbacks from herbivory can affect herbivore nutrition and population dynamics in positive or negative ways, depending on the spatial and temporal magnitude of herbivory and successional state of the ecosystem (Kerbes et al. 1990, Hik and Jefferies 1990, Pastor et al. 1997). Perhaps the most prominent feature of grazing systems are "grazing lawns", defined here as highly nutritious swards of grazing-tolerant graminoid vegetation, the structure of which is dependent on herbivory. Grazing lawns are typically associated with herbivores that express gregarious behavior, and colonial nesting geese have proven to be excellent models to study the interactions between herbivores and grazing lawns (McNaughton 1984, Cargill and Jefferies 1984, Bazely and Jefferies 1985, Kotanen and Jefferies 1987).

Studies on grazing lawns and lesser snow geese (*Anser c. caerulescens*) in the eastern Canadian subarctic have shown that nutrients recycled through goose feces are critical for the maintenance of rapid plant growth in heavily grazed swards (Cargill and Jefferies 1984, Bazely and Jefferies 1985; Ruess et al. 1989), and that grazing by geese may increase the nitrogen content of aboveground tissues (Bazely and Jefferies 1985, Kotanen and Jefferies 1987). However, the over-population of lesser snow geese has destroyed vast expanses of grazing lawns along the Hudson Bay and James Bay coasts (Kerbes et al. 1990), principally as a result of spring grubbing for belowground tissues. Gosling growth and survival declined coincident with increases in goose density (Cooch et al. 1993).

Gosling growth has been shown to be highly sensitive to the quality and availability of foods (Cooch et al. 1991, Larsson and Forslund 1991, Sedinger and Flint 1991, Lindholm et al. 1994). Geese have simple digestive systems that are inefficient at metabolizing foods high in fiber (Demment and Van Soest 1985). These digestive constraints are exacerbated in goslings, owing in part to esophageal volume constraints (Sedinger and Raveling 1988), metabolic requirements associated with some of the highest growth rates of precocial birds (Ricklefs 1973), and tundra vegetation that is low in sulfur-containing amino acids required for protein synthesis (Sedinger 1984). Research has shown that the size of goslings at fledging influences first-year survival, adult body size, breeding probability, and adult fitness (Cooch et al. 1993, Larsson and Forslund 1991, Sedinger et al. 1995, Sedinger et al. *in press*). It follows that feedbacks

between herbivores and vegetation may have impacts on the demography and size of herbivore populations (Oesterheld et al. 1992, Cooch et al. 1993).

I studied the interactions between vegetation and Pacific Black Brant geese (*Branta bernicla nigricans*) (hereafter brant), and of the foods on which Cackling Canada geese (*Branta canadensis minima*) (hereafter cackling geese) rely while breeding in southwestern Alaska on the Yukon-Kuskokwim Delta. Recent attention has focused on the impacts of increased abundance of geese breeding in northern latitudes and the impacts they have had on their breeding grounds (Abraham and Jefferies 1997). Similarly, there has been growing concern over the effects of elevated atmospheric CO_2 and the associated feedbacks on atmospheric temperature, vegetation green-up patterns in northern latitudes (Keeling et al. 1996), and increased storm activity in the Bering Sea region (Serreze et al. 1997). This work is framed within these contemporary boundaries in an attempt to elucidate how abiotic and biotic conditions and events may affect the interactions between geese and the plant communities on which they rear their young.

The objective of the first study was to decouple the effects that forage quality and availability have on captive cackling gosling development. I exploited a seasonal decline in vegetation quality by staggering the collection of early- and late-hatching goslings, and further exploited each of these groups by using the selective foraging behavior of goslings to manipulate the availability of preferred foods within a mosaic of community types known to be important cackling goose brood-rearing habitat. This enabled me to contrast the growth of both early- and late-hatching goslings reared in high and low nutrient availability environments.

My second objective was to examine, and contrast, spatial and temporal variation of *Carex subspathacea* grazing lawns within two breeding brant colonies that had experienced different population dynamics over recent decades. *C. subspathacea* is critical forage for brant maintenance and growth, and brant demonstrate intra- and interannual faithfulness to brood rearing areas (Lindberg and Sedinger 1998). I measured the natural variation in grazing pressure and consumption on several brood rearing areas, within each of these colonies. I also examined the effect of grazing on forage availability, nutritional characteristics, and the growth response of *C. subspathacea* within a growing season using short-term and seasonal exclosures.

In the third chapter I examine the effects of density dependence on plant community zonation within the Tutakoke River brant colony, and the associated feedbacks to gosling size, and population dynamics. This work coupled a manipulative experiment that artificially created grazing lawns from ungrazed *C. ramenskii* meadows, with long-term data on changes in the areal extent of the dominant plant communities within this landscape. I present evidence that gosling mass has increased over the past six years despite observed density dependent features in this population, suggesting that brant grazing could result in a positive numerical response of this population within the next two decades.

My fourth objective was to examine the effects of chronic tidal flooding on salt marsh soil processes, and on plant communities known to have important life history implications to brant geese. To accomplish this I artificially flooded the dominant plant communities at the Tutakoke River brant colony with tidal waters in the field. This work

also allowed the examination of the interactions between natural grazing pressure and tidal flooding on soil processes and aboveground vegetation within grazed- and protected plots that were flooded at different frequencies for two growing seasons.

CHAPTER 1. Cackling Canada gosling growth: Separating variation in food quality from availability[1]

ABSTRACT

We decoupled the effects of forage quality and availability on the growth of captive Cackling Canada goslings (*Branta canadensis minima*) reared on the Yukon-Kuskokwim Delta, Alaska. Goslings were collected during the beginning of hatch and also six days later near the end of hatch such that gosling age reflected environmental forage quality, as measured by vegetation nitrogen content. Each of these groups were subdivided into high- and low- forage availability treatments. High-food availability goslings were allowed to graze within ungrazed enclosures before the low-food availability goslings grazed within the same enclosures. An 11% decline in the nitrogen content, averaged over key forage species, and throughout five day increments of the growing season, translated to an approximate 100 g decrease in mass of late hatching goslings at 31days-of-age. Late-hatching goslings reared in high-availability environments could not fully compensate for seasonal declines in forage quality by increasing intake rates; thus, it is advantageous for geese to nest early because forage quality exerts a stronger effect on gosling growth than does availability. Availability of foods resulted in additive effects on gosling growth when compared to seasonal declines in forage quality.

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Key words: Branta canadensis minima; *growth; compensation; hatch date; grazing*

INTRODUCTION

The nutritional environment experienced by growing young has important life history consequences. Gosling growth rates are among the highest of precocial birds (Ricklefs 1973, Sedinger 1986). In contrast to altricial species, gosling protein requirements are derived from plant tissues (Owen 1980), which are low in nitrogen relative to a diet that incorporates animal tissue (Sedinger 1992). The need to meet protein requirements is exacerbated by volumetric constraints of the digestive system of geese (Sedinger and Raveling 1988). Thus, geese breeding in northern latitudes are excellent models for answering questions regarding the environmental effects on growth of young because their breeding season is compressed. Research has suggested that variation in the quality of foods influences gosling mass and the structural size of young at fledging (Cooch et al. 1991, Larsson and Forslund 1991, Sedinger and Flint 1991, Lindholm et al. 1994) and that size at fledging is positively correlated with juvenile and adult survival, breeding probability, and future fecundity (Owen and Black 1989, Sedinger et al 1995).

Plant nitrogen decreases, relative to its fiber concentration, throughout the growing season (Chapin et al. 1980, Sedinger and Ravling 1986) and plant phenology has been reported to affect gosling growth (Cooch et al. 1991, Sedinger and Flint 1991). However, seasonal decline in the quality of foods covaries with reduced availability of key forage species because grazing pressure increases throughout hatch and brood rearing (Cargill and Jefferies 1984, Person et al. 1998). Thus, a complete understanding of hatch date effects on gosling size requires decoupling the effects of food quality and quantity.

Lindholm et al. (1994) found that seasonal variation in vegetation quality affected gosling growth and that augmenting gosling diets with duck chow, thereby increasing the availability of dietary protein, resulted in goslings that were larger than those reared in the wild. Growing young face growth limitations due not only to a phenological decline in the quality of forage, but also to decreased availability of food items because of increases in *per capita* grazing pressure throughout and post hatch. Thus, early hatching goslings not only feed on the highest quality vegetation, but they also have first access to preferred foods. Grazing can ameliorate seasonal declines in forage nitrogen content, but the realized benefits to consumers are dependent on the frequency of grazing bouts and productivity of vegetation (Cargill and Jefferies 1984, Person et al. 1998). Also, brood-rearing areas can differ in both the quality and availability of forage, irrespective of within-season grazing pressure (Gauthier et al. 1995, Person et al. 1998). Few studies to date have reported spatial variation in gosling growth associated with direct measures of spatial variation in forage, and aside from Cooch et al. (1993), these findings came from colonies that were broadly geographically separated (Black et al. 1997, Sedinger et al. 2001). Cooch et al. (1993) noted that Lesser Snow Geese (*Anser c. caerulescens*) maintained within- and among-season faithfulness to brood rearing areas that had been largely depleted of vegetation. Similarly, Black Brant (*Branta bernicla nigricans*) (hereafter Brant) and Greater Snow Geese (*Chen caerulescens atlantica*) demonstrate both within- and among-season faithfulness to brood rearing areas (Hughes et al. 1994, Lindberg and Sedinger 1998). Faithfulness to brood rearing areas that vary spatially in

habitat quality likely result in spatial variation in the growth rates of goslings within a breeding population (Aubin et al. 1993).

We decoupled the effects food quality and availability on growth rates of human-imprinted Cackling Canada Goose goslings (*Branta canadensis minima*) (hereafter Cackling geese). We exploited seasonal declines in the quality of vegetation by staggering the collection of early- and late-hatching goslings. We then assigned half of each treatment group to either high- or low availability treatments. Availability of forage was manipulated by first allowing the high availability group to 'precondition' the plot for the low availability group. Hence, the high availability treatment goslings always experienced largely ungrazed forage within enclosures. We hypothesized that there was a seasonal decline in forage quality and that this would translate into a decrease in gosling mass. Similarly, we tested the effects of forage availability on gosling growth and predicted that decreased availability would translate into smaller goslings after controlling for the quality of foods (Figure 1).

METHODS

STUDY AREA

This study was conducted in 1998 on the upper Kashunuk River on the Yukon Delta in southwestern Alaska. Cackling geese rear their young in brood-rearing areas where they primarily feed on *Triglochin palustris* which is conspicuous in grazing lawns comprised of several heavily grazed graminoid species that constitute pond margins. These grazing lawns are dominated also by grazing morphs of *Dupontia fisherii*, *Puccenellia*

phryganodes, *Carex subspathacea*, and *Stellaria humifusa* (B. T. Person unpub. data), and patches range in size from a few square meters to tens of meters depending on water-body size and depth, and substrate type. Adult and gosling Cackling geese also forage within *C. mackenzeii*- and *C. ramenskii*-dominated wet meadows where *T. palustris* can be abundant (Babcock and Ely 1994). Esophageal contents from goslings feeding in these vegetation types have shown *T. palustris* and *C. mackenzeii* leaves to be important components of Cackling gosling diets before fledging (Sedinger and Raveling 1984). Both the availability and quality of forage varies spatially among brood rearing areas used by Cackling geese in the upper Kashunuk river region (C. A. Babcock unpub. data).

GOSLING COLLECTION, MEASURMENTS, AND CARE

To examine the effects of forage quality on gosling growth we exploited the decline in plant tissue quality that occurred with date. We nest-searched and followed 350 Cackling nests to their hatch day. We collected one pipped egg, or dry gosling from each of 25 nests within the first two (early-hatching = "Eh"), and last three days (late-hatching = "Lh") of the total hatching period, defined by 90% of the nests hatching in the upper Kashunuk river drainage. Early-hatching goslings were collected on June 22, and the Lh treatment goslings were collected six days later on June 28. We define 'hatch' as any gosling that had broken its outer egg membrane. The majority of Lh goslings were collected as dry goslings, whereas an additional 24 h was required before most of the Eh goslings were dry: this slightly reduced age and effective hatch date differences between our early- and late-hatch treatments. All hatched goslings were marked with a webtag and thereafter weighed (± 5 g) daily using a top loading scale. Every three days we

measured exposed culmen, head length, and the left tarsus bone (± 0.1 mm) using dial calipers of all goslings. We also noted the date of eruption, and thereafter measured ninth primary length every three days following methods of Dzubin and Cooch (1992). All goslings were housed in pens within a non-insulated structure between 24:00 and 05:00 hours daily and walked to nearby treatment plots for experimental manipulations that typically were conducted daily between 06:30 and 17:00, after which time they were walked to, and allowed to free range in areas distant from our experimental plots.

Within 24 hours of hatching, goslings were taken to habitat similar to those used by wild broods (Sedinger and Raveling 1988, Babcock and Ely 1994). Goslings were allowed to free-range within the same habitats as those used in our experiment for approximately 10 h d^{-1}, in different areas, during the first 8 days of their lives. When weather was inclement and during the evening hours we supplemented their diet with large turves of vegetation. Goslings also fed on a mix of pelleted alfalfa and duck starter that was ground into a powder (N = %1.6 ± 0.2, C:N = 22 ± 3) (data represent SE of the mean). Goslings had access to fresh water except between the hours of 03:00 and 05:00 hours prior to daily weighing.

TREATMENT ASSIGNMENT AND SAMPLE SIZE

As mentioned above, forage quality was manipulated by exploiting variation in hatch date (*i.e.*, six days in our experiment) in the upper Kashunuk River drainage, which allowed us to create both high quality (early-hatching, Eh) and low quality (late-hatching, Lh) treatment groups of goslings. Each of these forage quality treatment groups was divided into high (Ha) and low (La) availability treatments when goslings were five days

old. To accomplish this, we ranked all goslings within each Eh and Lh group into five size categories based on tarsal length. We chose this trait for treatment assignment because it has been reported to be highly correlated with future adult tarsus measurements (Cooch et al. 1991). We then randomly picked a number between zero and six and assigned the corresponding gosling from each size class to either the high availability (Ha) or low availability (La) treatment groups. This ensured that within hatch date, treatment groups did not differ in tarsal length at the beginning of the experiment.

Twelve and eight goslings died from exposure in the Eh and Lh treatment groups, respectively; therefore, our sample sizes were: 7(EhHa), 6 (EhLa), 9 (LhHa), and 8 (LhLa). No mortality occurred after treatments began. Late-hatching treatment groups consisted of larger (culmen, 1.3 ± 0.3 mm; head length, 2.4 ± 0.3 mm; tarsus 0.8 ± 0.3 mm) and heavier (4.6 ± 1.0 mm) goslings than those hatching early at the onset of the experiment. These differences could only reduce the magnitude of the treatment effects that we document below.

Food availability to goslings in the La treatment group was manipulated by using goslings in the Ha treatment group. We established eight and six temporary enclosures for the early and late hatching treatment groups, respectively, throughout the season. High availability goslings were allowed to freely graze within the enclosures for five days before we moved them to a newly established ungrazed enclosure. We then placed the low availability goslings within the preconditioned enclosure and allowed them to forage on the remaining vegetation. We hypothesized that the high availability goslings would preferentially feed on the highest quality vegetation and in so doing decrease the

abundance of preferred species. Each enclosure represented a mosaic of vegetation types exploited during brood rearing and contained grazing lawns, *C. ramenskii*, and *C. mackenzeii* dominated communities. Mean enclosure size was 200 and 230 m^2 for the early and late hatching treatment groups, respectively, and care was taken to ensure equal extent of all three community types relative to the number of goslings (Table 1). Enclosures were larger for the late hatching treatment groups to accommodate for the increase in grazing pressure because those treatment groups were larger than the early hatching groups. All enclosures contained ponds so goslings had access to water for bathing and drinking. Experiments were conducted from June 22 to July 29, 1998, after which time goslings were killed using methoxyflourine. Animal care procedures were approved by *The Institute of Animal Care and Use Committee*, University of Alaska, Fairbanks.

VEGETATION SAMPLING AND NUTRITIONAL ANALYSIS

We measured the areal extent of grazing lawns, *C. ramenskii*, and *C. mackenzeii* plant communities within each enclosure when enclosures were established. We then sampled five random 10 cm^2 turves within each of these communities at the time enclosures were established (T0), following five days of grazing by the high availability goslings (T1), and again after the low availability goslings had fed within enclosures for five days (T2). All standing vegetation was clipped to the soil surface and separated into live and dead. We did not sort the remaining live vegetation that comprised the grazing lawn community to species but collected it for estimating its live standing biomass and nutritional content throughout the season. Thus, when we refer to 'grazing lawn'

hereafter we refer to the remaining green biomass after *T. palustris* had been removed. We separated vegetation within the *C. ramenskii* and *C. mackenzeii* communities into grasses, sedges, forbs, woody, and standing dead vegetation. All plant material was dried in a field laboratory at 60° C, and later redried and weighed (± 0.01 g) at the University of Alaska in Fairbanks. We sorted a subset of the sedge samples (n=20 for each community type) and determined that 89% of the sedges from the *C. ramenskii* and 95% of the sedges from the *C. mackenzeii* communities were *C. ramenskii* and *C. mackenzeii*, respectively. We followed the classification system of Hultén (1990).

We measured seasonal changes in vegetation nitrogen and carbon only on samples collected every five days throughout the experiment (23 June to 28 July, 1998). Plant samples were ground through a 20 mesh size Willey Mill and combusted in a LECO autoanalyzer (Michigan, MI) to estimate carbon and nitrogen content of key food items collected throughout the season. Linear regression was used to predict changes in plant N and C content over time. Nitrogen and C content of vegetation collected within these five-day intervals was predicted using the equations developed from the linear regression models. We pooled *T. palustris* biomass collected from each of the three communities on which we focused to estimate its nitrogen and carbon content because there was insufficient standing crop biomass (SCB) to independently estimate its nutritional content from each community. Standing crop nitrogen (SCN) and standing crop carbon (SCC) were calculated by multiplying the nitrogen and carbon content of vegetation by live standing crop biomass, respectively. We present SCN and SCC of *T.* palustris, sedges collected from the *C. ramenskii* and *C. mackenzeii* communities, and the

remainder of green vegetation that comprised grazing lawns after *T. palustris* had been removed from these samples. We calculated offtake of *T. palustris*, *C. mackenzeii*, *C. ramenskii*, and grazing lawn by Ha goslings by subtracting T1 biomass from T0 biomass for each community type. Similarly, offtake by La goslings was estimated by subtraction of T2 biomass from that of T1. Nitrogen and carbon offtake was calculated by substituting estimates of SCN and SCC for SCB estimates in the above formula, respectively.

STATISTICAL PROCEDURES

Seasonal changes in the nutritional content of vegetation were modeled by linear regression (PROC REG) (SAS Institute Inc., 1990). Similarly, we tested for seasonal changes in the availability of SCB, SCN, and SCC in plots that were initially established (T0) using linear regression. Because *T. palustris* and sedges occur in more than one plant community, we conducted analyses for each community type. We tested for treatment effects on the availability of SCB, SCN and SCC using ANOVA (PROC GLM) by entering plot nested within community type, and we included treatment and species as class variables. If an overall treatment effect was detected, at alpha = 0.05, we used Tukey's honest significant difference (HSD) multiple comparison method to determine which treatments differed. If a significant species effect was found we limited our analysis to a particular species (*e.g.*, *T. palustris*) and tested for treatment differences in availability. Similarly, treatment variation in SCB, SCN, and SCC offtake were evaluated using ANOVA procedures followed by Tukey's HSD multiple comparison method if an overall treatment effect was found.

We tested for treatment effects on gosling mass, tarsus, culmen, ninth primary, and head length using PROC Mixed model procedures (SAS Institute Inc., 1990). We entered treatment, time, individual, and sex as class variables. We entered gosling age as a continuous variable. Treatment by age interactions were used to test for differences in mass and structural characteristics. When a significant interaction was found we performed linear contrasts to decouple treatment variation. Our random statement in these models consisted of individuals nested within treatment, and we modeled our correlation structure as an autoregressive process of order one. Mass and structural measurements were $\log_{10}$ transformed and ninth primary measurements were $\log_{10} + 1$ transformed to meet model assumptions. All data presented herein represents the mean ± 1 standard error of the mean unless otherwise noted.

RESULTS

VEGETATION QUALITY, AVAILABILITY, AND OFFTAKE

Nitrogen content declined throughout the season for all forage species that we sampled, with the exception of the remaining green vegetation that comprised the grazing lawn. The nitrogen content of this mixed species grazing lawn did not change throughout the growing season ($P = 0.41$; $r^2 = 0.02$) and generally had the lowest nutritional characteristics of all foods (1.9 ± 0.1 %N, 42.4 ± 0.2 %C). *T. palustris* had the highest nitrogen content of all forage species, and it declined from 4.0 ± 0.2 to 3.5 ± 0.4 % between June 26 and July 27 ($P = 0.008$; $r^2 = 0.28$) (Figure 2). *C. mackenzeii* had a higher nitrogen content than did *C. ramenskii*, and this difference remained as their

nitrogen concentration declined throughout the growing season (*C. mackenzeii*: $P < 0.0001$; $r^2 = 0.48$) (*C. ramenskii*: $P < 0.0001$; $r^2 = 0.42$) (Figure 2). Carbon content of *C. mackenzeii*, *C. ramenskii*, and grazing lawns tended not to change throughout the growing season (all *P* values >0.5). However, the C concentration of *T. palustris* declined from 44 to 38 % throughout the growing season ($P < 0.0001$; $r^2 = 0.46$). The rates at which carbon and nitrogen content of *T. palustris* declined differed slightly and we detected a seasonal increase in the ratio of these two variables (C:N = -1.3 + (0.065 x Julian date), suggesting that the nitrogen content of this forage was also diluted with carbon although this relationship was not statistically significant ($P = 0.08$; $r^2 = 0.11$).

Availability of *T. palustris* SCB, SCN, and SCC did not differ among enclosures that were first established for either the early or late hatching high availability treatments (all *P* values > 0.5). Availability of sedge SCB increased throughout the season in the *C. mackenzeii* ($P = 0.006$) and *C. ramenskii* communities ($P = 0.07$). Similarly, sedge SCC increased in each of these communities. Sedge SCN availability did not change throughout the season in plots that were initially established. In contrast, SCB, SCN and SCC availability of the grazing lawn tended to decline throughout the season although these relationships were not significant (all *P* values > 0.06).

T. palustris SCB for LhLa treatment goslings was slightly greater than that to which EhHa goslings were first offered which, in essence, makes our results of food quality effects on gosling growth conservative ($F_{1,168} = 3.9$; $P = 0.049$). We did not detect a difference in *T. palustris* SCB between these two treatments when communities were analyzed separately (Table 2). Standing crop nitrogen and SCC of *T. palustris* did

not differ between these two treatments, although available SCC was slightly greater for the LhHa goslings ($F_{1,168} = 3.8$; $P = 0.052$). Similarly, availability of *T. palustris* SCB, SCN, and SCC did not differ among treatments either at the time birds were first placed in enclosures (T1) nor following five days of grazing within enclosures (T2) (all P values > 0.3). Availability of the remaining grazing lawn SCB, SCN, or SCC did not differ between either set of early- and late-hatching availability treatments (all P values > 0.39). Late-hatching high availability goslings were reared in environments that had greater availability of *C. mackenzeii* SCB and SCC than were EhHa treatment goslings (SCB:$F_{1,66} = 7.8$; $P = 0.006$, SCC:$F_{1,66} = 7.7$; $P = 0.007$) (Table 3). Availability of *C. ramenskii* and *C. mackenzeii* sedge SCB, SCN, and SCC did not differ between either early- or late-hatching high and low availability treatments (all P values > 0.18) (Table 3). High and low availability treatment groups within both early- and late-hatching groups were reared in environments that differed in available SCB, SCN, and SCC. High availability treatments were consistently reared in environments with a greater availability of SCB, SCN, and SCC of all foods that we focused on than were goslings in either low availability treatments (Table 2 and 3).

Early- and late-hatching high availability treatments removed more *T. palustris* SCB, SCN, and SCC than did the Eh and Lh low availability goslings (all treatment P values < 0.0001) (Table 4). Similarly, offtake of both sedge and grazing lawn SCB, SCN, and SCC tended not to differ between early- and late-hatching high availability treatment groups. Late-hatching high availability goslings consistently removed more

sedge and grazing lawn SCB, SCN, and SCC than did the EhHa treatment goslings (Table 4).

ENVIRONMENTAL EFFECTS ON GOSLING GROWTH

We found significant variation in gosling mass and structural characteristics associated with our treatments (Table 5). Goslings that hatched six days earlier were nearly 100 g heavier and structurally larger at 31-days of age (Figure 3). Male goslings were structurally larger, but not significantly heavier than female goslings (Table 5). Male goslings were on average 50 g heavier than female goslings when averaged across treatments. However, our LhLa treatment resulted in females that were 50 g heavier than male goslings. This effect was strongly influenced by one female gosling, that despite environmental pressures, was the largest of all goslings in our experiment. Availability of preferred forage affected gosling mass and structural size such that goslings that fed within previously grazed enclosures were both smaller and lighter than birds reared in high availability environments (Figure 3). Early-hatching low availability gosling growth did not differ from LhHa treatment goslings; thus, the effect of availability of preferred foods (predominantly *T. palustris*) was of the same magnitude as that of hatch date effects (Figure 3).

Ninth primary growth began when goslings were 27 ± 3 days of age regardless of hatch date, forage availability, or gosling sex. However, feather growth was affected by hatch date and forage availability by the time goslings were 31 days old (Table 5). Ninth primaries of early-hatching goslings were 15.6 ± 1.3 mm and 10.2 ± 1.4 mm for high and low availability treatment groups, respectively ($P = 0.008$). Hatch date and availability of

forage had effects on ninth primary growth similar to those seen for mass and other structural characteristics. Feather growth of EhLa goslings did not differ from LhHa gosling which had a mean ninth primary length of 8.3 ± 1.1 mm. LhLa gosling ninth primaries were smaller (5.3 ± 1.2 mm) than all other treatments.

DISCUSSION

ENVIRONMENTAL EFFECTS ON GOSLING GROWTH

Our experiment distinguishes the effects of forage quality and quantity on gosling growth, and our findings indicate that each of these factors have proportionally similar consequences for gosling growth and size at fledging. We demonstrated that vegetation nitrogen content significantly declined throughout the season, and because of this, late hatching goslings fed on vegetation that was lower in quality relative to vegetation consumed by early-hatching goslings (Figure 2). The effects of forage quality on gosling growth are evident from two independent contrasts that compare food quality effects within the same availability treatments; (EhHa *vs.* LhHa and EhLa *vs.* LhLa) (Tables 1, 2 and 3). EhHa goslings were significantly heavier and structurally larger than LhHa goslings. Similarly, EhLa goslings were significantly larger and heavier than LhLa goslings (Figure 3). We used grazing, by high availability treatment goslings, to reduce the availability of preferred foods presented to low availability goslings. In so doing we were able to 1) distinguish between the effects of quality and availability on growth of goslings and 2) manipulate, at the plot level, the abundance of preferred resources which enabled us to draw inferences on the effect spatial variation in brood rearing habitats

likely has on gosling development. Both Eh and Lh goslings reared on these preconditioned swards were significantly smaller than Eh and Lh high availability goslings (Table 4). The effects of forage quality and availability had similar consequences for the size of Cackling goslings, but we argue below that forage quality has greater ecological importance to gosling growth because LhHa goslings could not compensate for seasonal declines in forage nitrogen by increasing intake rates.

We believe our results from 31 day-old goslings can be extrapolated to effects at fledging, and that our experimental design simulates conditions experienced by wild goslings. The inability of our imprinted goslings to compensate for reduced forage quality and availability simulates natural conditions for several reasons. First, forage quality declined throughout the season. Second, increased grazing pressure throughout the brood rearing season reduces the availability of key foods within brood rearing areas (Sedinger and Raveling 1986, Gauthier et al. 1994, Person et al. 1998). And third, because broods show intra-annual faithfulness to brood rearing areas, they are, in essence, not only constrained by their hatch date, but also their environment (Cooch et al. 1993, Lindberg at al. 1998). We argue that these conditions would preclude compensatory growth of either goslings hatching late, or of those reared in areas with low availability of preferred foods.

QUALITY EFFECTS ON GROWTH OF GOSLINGS

Late-hatching goslings on average fed on *T. palustris* that had 3.5 % less nitrogen concentration than did early-hatching goslings (Figure 2). Similarly, late-hatching goslings fed on *C. ramenskii* and *C. mackenzeii* tissues that had *ca.*15% less nitrogen concentration than did early hatching goslings. The treatment effect of hatch date in this experiment translates to an 11% decline in forage N concentration when averaged across the 3 forage species throughout the growing season. Thus, a six day delay in hatch-date translated to goslings that were approximately 100 g lighter compared with first-hatched goslings in the upper Kashunuk River drainage (Figure 3).

Late-hatching goslings did not compensate for seasonal declines in food quality despite increased N intake. Within our high availability treatments, early- and late-hatching goslings experienced environments with the same available standing crop biomass of *T. palustris*, the most preferred forage species (Table 2). However, late-hatching goslings removed 16.7 ± 4.2 g dwt^{-1} m^{-2} d^{-5} compared to 7.3 ± 3.7 g dwt^{-1} m^{-2} d^{-5} *T. palustris* SCN removed by early-hatching goslings. One consequence of this is that late-hatching birds removed more SCC, 312.3 ± 99.7 g dwt^{-1} m^{-2} d^{-5}, than did early-hatching goslings which removed 78.4 ± 79.3 g dwt^{-1} m^{-2} d^{-5} *T. palustris* SCC. Thus, growth of goslings was negatively correlated with carbon intake. Despite removing nearly twice as much nitrogen on an area basis, late-hatching birds foraged on vegetation with a substantially higher C:N ratio, a metric that is negatively correlated with forage digestibility (Gadallah and Jefferies 1995a,b). This problem was exacerbated by increased intake of *C. mackenzeii* and *C. ramenskii* after *T. palustris* SCB was reduced to

approximately 7 g m^{-2}. Thus, once a gosling fed on these species, their diet was of lower quality because *C. mackenzeii* and *C. ramenskii* have C:N ratios of 19.9 ± 1.1 and 19.6 ± 0.8, respectively, compared to 11.3 ± 0.4 for *T. palustris*.

FORAGE AVAILABILITY

Forage availability strongly affected gosling growth and individuals that were reared in low availability environments were smaller (Figure 3). Goslings showed a strong preference for *T. palustris*, which had the highest nitrogen content of all forage species in this study (Figure 2, Table 2). Preference for *T. palustris* by Cackling goslings has been demonstrated previously (Sedinger and Raveling 1984, 1986, 1988), and mass of goslings was positively correlated with *T. palustris* offtake in this study. High availability goslings were reared in environments that initially had *ca.* 25 g m^{-2} more *T. palustris* SCN than low availability treatment goslings when averaged across the season. *T.* palustris SCB was 10 and 8 g dwt. m^{-2} lower for the early- and late-hatching La treatments when compared to Ha environments (Table 2).

Several studies have described spatial variation in forage quality and availability of brood rearing areas (Gauthier et al 1995, Person et al. 1998). Results from studies on spatial variation in *C. mackenzeii* and *T. palustris* in the upper Kashunuk River drainage suggest that some brood rearing areas have both lower availability and quality of these foods when compared to other brood rearing sites (Babcock and Ely 1994, C.A. Babcock unpub. data). Availability of key foods following preconditioning of the vegetation within enclosures in this experiment was similar to variation observed in the wild, although the frequency at which vegetation was grazed in our experiment was likely

higher than under natural conditions. Vegetation capable of rapid regrowth following grazing tends to be of higher quality than ungrazed vegetation (Cargill and Jefferies 1984). However, the magnitude of benefit to consumers is also dependent on the growth rate of vegetation, and, over the short term, intensive grazing typically reduces SCB of preferred foods if the frequency of grazing bouts is high (Gauthier et al. 1995, Person et al. 1998, Piedboeuf and Gauthier 1999). Our low availability treatments likely simulated the consequences of both density-dependence and spatial variation in food availability among brood rearing habitats, supporting the notion that spatial variation in Cackling gosling growth due to variation in abundance of key food plants exists among brood rearing areas (C.A. Babcock unpub. data).

Smaller, late-hatching goslings may have fed less efficiently than larger early-hatching goslings for several reasons. First, SCB of less preferred species increases throughout hatch and the early brood rearing period as the proportion of *T. palustris* SCB within swards declines, thus making it difficult for late-hatching goslings to find *T. palustris*. Second, the availability of preferred foods is reduced from increased grazing pressure. Offtake of sedges and grazing lawn tended not to differ among treatments, although LhLa goslings removed significantly less sedge and grazing lawn biomass than all other treatments despite its high availability (Table 4). Limits in gut capacity ultimately precluded small goslings from selecting plants that have higher fiber content. Sedinger and Raveling (1988) argued that processing time by the gizzard limits intake, making non-feeding bouts necessary to empty esophageal contents. Further, environmental conditions experienced by both late-hatching and goslings reared in low

availability environments exacerbate low digestive efficiency because digestibility is inversely related to the amount of fiber in the diet (Gadallah and Jefferies 1995a,b). Smaller goslings are less efficient at retaining dietary energy and protein then are larger goslings because guts length scales linearly while mass-specific protein requirements are higher in smaller-bodied birds (Demment and Van Soest 1985, Sedinger 1997). This has a trade-off though; gut size can only be so big because nitrogenous losses from intestinal sloughing are likely greater than fecal nitrogen would predict due to the biological value of animal versus plant nitrogen. That is, vegetation is low in the sulfur-containing amino acids cystein and methionine, and gut cells are likely not low in these amino acids (Sedinger 1984).

POTENTIAL IMPLICATIONS FOR CLIMATE AND POPULATION DYNAMICS

Our results suggest that it is advantageous for geese to nest as early as possible because forage quality has stronger effects than forage quantity on the growth of young. Late hatching goslings reared in an environment with high resources could not compensate for declines in the quality of foods, suggesting that even if a late hatching brood were reared in a habitat with abundant forage resources, its body size would still be smaller than if it had developed earlier in the season. Because size at fledging is positively correlated with first year survival, breeding probability, and fecundity of Brant, age of first breeding in Barnacle geese (*Branta leucopsis*), survival and recruitment rates in Lesser Snow geese (Cooch et al. 1991, Cooch et al. 1993, Larsson and Forslund 1991, Sedinger *et al.* 1995, Larsson *et al.* 1998, Sedinger et al. *in press*), selective pressures to nest early are high in waterfowl that breed and rear their young in northern latitudes. However, directional

selection pressures towards early migration are counterbalanced by wintering ground effects and climactic events on the breeding grounds. Geese must acquire sufficient body reserves on the wintering grounds to meet energetic requirements for spring migration and clutch formation (Lessells et al. 1979, J. Schamber unpub. data). However, breeding success of geese breeding in northern latitudes is also strongly affected by spring climatic events on the breeding grounds where, at the extreme, snow cover sometimes persists so long that geese fail to nest (Skinner et al. 1998).

Recent attention has focused on the effects of a changing climate in response to increased atmospheric CO_2 on the timing of vegetation green-up in northern latitudes (Keeling et al. 1996). Crick and Sparks (1999) presented long-term data comparing timing of egg laying and spring temperatures of birds breeding in the United Kingdom and demonstrated a trend towards birds breeding earlier in the season. However, this work consisted of a broad inventory of breeding fauna and demonstrated that some species, notably larger-bodied species, failed to temporally shift their breeding patterns. Both and Visser (2001) demonstrated that species that migrate over long distances are less likely to respond to proximal (*e.g.*, climatic) cues and suggest this may be maladaptive. Our results suggest that if there were a decoupling of arrival to the breeding grounds by geese and vegetation green-up, the consequences to gosling growth would be significant. There is some evidence for these consequences in arctic nesting passerines (Eeva et al. 2000), who demonstrated that annual variation in prey density, relative to hatch, resulted in clutch size reduction of Siberian (*Poecile cinctus*) and Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*) as well as reduced fledgling success of

the Great Tit. While recent attention has focused on the impacts of increased abundance of geese breeding in northern latitudes and the adverse impacts they have had on their breeding grounds (Abraham and Jefferies 1997), we suggest that the context of density-dependence should be broadened to include variation in climate when evaluating interactions between breeding geese and the foods on which they rely.

In summary, an average 11% decline in the nitrogen content of key forage species throughout the growing season translated to an approximately 100 g decrease in mass of 31 day-old goslings. Moreover, goslings reared in environments with high forage availability could not compensate for seasonal declines in forage quality by increasing intake rates. Since forage quality exerts a stronger effect on gosling growth than does availability, it appears advantageous for geese to nest as early as possible. Forage availability however, is critical for the growth of Cackling goslings. Availability of foods resulted in proportionally similar effects on gosling growth when compared to differences in forage quality and it is likely that spatial variation in forage availability in this system has pronounced life history consequences for individuals.

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LITERATURE CITED

ABRAHAM, K. F. AND R. L. JEFFERIES. 1997. High goose populations: causes, impacts and implications. Pages 7-72 *in* B. D. J. Batt (ed.). Arctic ecosystems in peril: report of the Arctic goose habitat working group. Arctic Goose Joint Venture SpecialPublication. U. S. Fish and Wildlife Service, Washington D.C. and Canadian Wildlife Service, Ottawa, Ontario.

AUBIN, A. E., A. DZUBIN, E. H. DUNN, AND C. D. MACINNES. 1993. Effects of summer feeding area on gosling growth in Snow Geese. Ornis Scandinavia 24: 255-260.

BABCOCK, C. A. AND C. R. ELY. 1994. Classification of vegetation communities in which geese rear broods on the Yukon-Kuskokwim delta, Alaska. Canadian Journal of Botany 72:1294-1301.

BADZINSKI, S. S., C. D. ANKNEY, J. O. LEAFLOOR, AND K. F. ABRAHAM. 2002. Growth and development of Canada Geese and Lesser Snow Geese: Ecological adaptation or physiological constraint? Auk 119:in press.

BLACK, J.M., COOCH, E.G., LOONEN, M.J.J.E., DRENT, R.H. & OWEN, M. (1997) Body size variation in barnacle goose colonies: evidence for local saturation of habitats. pp. 129-140. In F. Mehlum, J.M. Black & J. Madsen (eds.), Research on Arctic Geese, vol. Skrifter 200, Norsk Polarinstitutt, Oslo.

BOTH, C. AND M. E. SPARKS. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 296-298.

CHAPIN F. S., D. A. JOHNSON, AND J. D. MCKENDRICK. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: Implications for herbivory. Journal of Ecology 68:189-209.

COOCH, E. G., D. B. LANK, A. DUZBIN, A., R. F. ROCKWELL, AND F. COOKE. 1991. Body size variation in Lesser Snow Geese: seasonal variation in gosling growth rate. Ecology 72:503-512.

COOCH, E. G., JEFFERIES, R. L., ROCKWELL, R. F., AND F. COOKE. 1993. Environmental change and the cost of phylopatry: an example in the lesser snow geese. Oecologia 93: 128-138.

CRICK, Q. P., AND T. H. SPARKS. 1999. Climate change related to egg-laying trends. Nature 399: 423-424.

DEMMENT, M. W. AND P. J. VANSOEST. 1985. A nutritional explanation for body-size patterns of ruminant and non ruminant herbivores. American Naturalist 125:641-672.

DUNN, E. H. AND C. D. MACINNES. 1987. Geographic variation in clutch size and body size of Canada geese. Journal of Field Ornithology 58:355-371.

DZUBIN, A. AND E. G. COOCH. 1992. Measurements of geese: general field methods. California waterfowl association, Sacramento, California.

EEVA, T., VEISTOLA, S. AND E. LEHIKOINEN. 2000. Timing of breeding in subarctic passerines in relation to food availability. Canadian Journal of Zoology 78: 67-78.

GADALLAH, F. L. AND R. L. JEFFERIES. 1995a. Forage quality in brood rearing areas of the lesser snow goose and the growth of captive goslings. Journal of Applied Ecology 32:276-287.

GADALLAH, F. L. AND R. L. JEFFERIES. 1995b. Comparison of the nutrient contents of the principal forage plants utilized by lesser snow geese on summer breeding grounds. Journal of Applied Ecology 32:263-275.

GAUTHIER, G., R. J. HUGHES, A. REED, J. BEAULIEU, AND L. ROCHEFORT. 1995. Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). Journal of Ecology 83:653-664.

HUGHES J. R., A. REED, G. GAUTHIER. 1994. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. Journal of Wildlife Management 58:536-545.

HULTÉN E (1990) Flora of Alaska and neighboring territories. A manual of the vascular plants. Stanford University Press, Stanford, California.

KEELING, C. D., J. F. S. CHIN, AND T. P. WHORF. 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. Nature 382:146-149.

LARSSON, K., H. P. VAN DER JEUGD, I. T. VAN DER VEEN, AND P. FORSLUND. 1998. Body size declines despite positive directional selection on heritable size traits in a Barnacle goose population. Evolution 52:1169-1184.

LARSSON, K. AND P. FORSLUND. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:679-686.

LEAFLOOR, J. O., D. A. ANKNEY, AND D. H. RUSCH. 1998. Environmental effects on body size of Canada geese. Auk 115:26-33.

LESAGE, L. AND G. GAUTHIER. 1998. Effect of hatching date on body and organ development in greater snow goose goslings. Condor 100:316-325.

LESSELLS, C. M., SIBLY, R., OWEN, M., AND S. ELLIS. 1979. Weights of female Barnacle geese during breeding. Wildfowl 30:72-74.

LIGHTBODY, J. P. AND C. D. ANKNEY. 1984. Seasonal influence on the strategies of growth and development of canvasback and lesser scaup ducklings. Auk 101:121-133.

LINDBERG M.S., AND J. S. SEDINGER. 1998. Ecological significance of brood-site fidelity in Black Brant: Spatial, annual, and age-related variation. Auk 115:436-446.

LINDHOLM, A., G. GAUTHIER, AND A. DESROCHERS. 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting Greater Snow Geese. Condor 96:898-908.

OWEN, M. 1980. Wild geese of the world. B. T. Batsford Ltd., London.

OWEN, M. AND J. M. BLACK. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. Journal of Animal Ecology 58:603-617.

PERSON, B. T., C. A. BABCOCK, AND R. W. RUESS. 1998. Forage variation in brood rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska. Journal of Ecology 86:243-259.

PIEDOEUF, N. AND G. GAUTHIER. 1999. Nutritive quality of forage plants for greater snow goose goslings: when is it advantageous to feed on grazed plants? Canadian Journal of Zoology 77: 1908-1918.

PROP, J. AND T. VULINK. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Functional Ecology 6:180-189.

RICKLEFS, R. E. 1973. Patterns of growth in birds. Growth rate and mode of development. Ibis 115:177-201.

RICKLEFS, R. E., AND S. WEREMIUK. 1977. Dynamics of muscle growth in the Starling and Japanese Quail: a preliminary study. Comparative Biochemistry and Physiology 56:419-423.

SAS INSTITUTE INC. 1990. SAS/STAT User's Guide, Release 6.04 edition. SAS Institute Inc., Cary, North Carolina.

SEDINGER J. S. 1984. Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. Journal of Wildlife Management 48:1128-1136.

SEDINGER, J. S., AND D. G. RAVELING. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295-306.

SEDINGER, J. S. 1986. Growth and development of Canada goose goslings. Condor 88:169-180.

SEDINGER, J.S., AND D. G. RAVELING. 1986. Timing of nesting by Cackling Geese in relation to the quality and availability of their food plants. Journal of Animal Ecology 55:1083-1102.

SEDINGER, J.S. AND D. G. RAVELING. 1988. Foraging behavior of cackling canada goose goslings: implications for the roles of food availability and processing rate. Oecologia 75:119-124.

SEDINGER, J. S. AND P. F. FLINT. 1991. Growth rate is negatively correlated with hatch date in Black Brant. Ecology 72:496-502.

SEDINGER, J. S. 1992. Ecology of prefledging waterfowl. *in* Ecology and management of breeding waterfowl. Batt, B. D. J. et al. University of Minnesota Press. Minneapolis, Minnesota.

SEDINGER, J. S., P. L. FLINT, AND M. S. LINDBERG. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404-2414.

SEDINGER, J. S. 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99:314-326.

SEDINGER, J.S., LINDBERG, M.S., PERSON, B.T., EICHHOLZ, M.W. AND P.L. FLINT. 1998. Density-dependence effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

SEDINGER, J. S., M. P. HERZOG, B. T. PERSON, M. T. KIRK, T. OBRITCHKEWITCH, P. P. MARTIN, AND A. A. STICKNEY. 2001. Large scale variation in growth of black brant goslings related to food availability. Auk 118: in press.

SEDINGER, J.S., LINDBERG, M.S., AND N. D. CHELGREN. 200X. Age-specific breeding probability in black brant: effects of population density. Journal of Animal Ecology 00: in press.

SKINNER, W. R., JEFFERIES, J.L., T.J. CARLETON, AND R. F. ROCKWELL. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. Global Change Biology 4:3-16.

Table 1.1. Mean (± 1 SE) areal extent of plant communities (m^2) within enclosures established for captive Cackling Canada gosling experiment. Enclosure size was increased for late hatching (Lh) treatments to accommodate larger sample size of goslings (n=17 for Lh compared to n=13 for early hatching treatment).

	Early hatching	Late Hatching
Community		
C. mackenzeii	35.3 ± 10.8	48.3 ± 20.3
C. ramenskii	55.0 ± 8.3	71.3 ± 18.2
Grazing lawn	46.7 ± 12.2	60.3 ± 18.0

Table 1.2. Available standing crop biomass (g dwt. m^{-2}) for Cackling Canada gosling experiment. Periods represent available biomass for: **T0** High availability (Ha) treatment groups, **T1** biomass remaining after Ha goslings preconditioned the plots for the Low availability treatments (La) and, **T2** corresponds to the amount of biomass remaining after La goslings fed on vegetation for *ca*. 5 days. Data represent the mean ± 1 SE of *T. palustris* within *C. mackenzeii* and *C. ramenskii* dominated meadows and grazing lawns found in the upper Kashunuk River drainage. Letters shared between early and late hatching treatments within time periods (*e.g.*, Eh T0 *vs.* Lh T0 etc.) are not statistically different at alpha > 0.05 (Tukey's HSD multiple comparison).

	Early Hatching treatments			Late Hatching treatments		
Period	T0	T1	T2	T0	T1	T2
Triglochin palustris						
in *C. mackenzeii*	3.96 ± 0.57 a	0.88 ± 0.17 a	0.66 ± 0.13 a	3.09 ± 0.52 a	1.62 ± 0.37 a	0.38 ± 0.09 a
in *C. ramenskii*	5.19 ± 0.87 a	3.55 ± 0.79 a	4.41 ± 0.74 a	5.52 ± 0.87 a	3.99 ± 0.56 a	2.77 ± 0.67 a
in grazing lawn	6.29 ± 0.84 a	1.24 ± 0.23 a	1.36 ± 0.26 a	7.73 ± 0.49 a	2.41 ± 0.31 a	1.39 ± 0.28 a

Table 1.3. Available standing crop biomass (g dwt. m^{-2}) for Cackling Canada gosling experiment. Periods represent available biomass for: **T0** High availability (Ha) treatment groups, **T1** biomass remaining after Ha goslings preconditioned the plots for the Low availability treatments (La) and, **T2** corresponds to the amount of biomass remaining after La goslings fed on vegetation for *ca.* 5 days. Data represent the mean ± 1 SE of sedges within *C. mackenzeii* and *C. ramenskii* dominated meadows and grazing lawns without *T. palustris* biomass included. Letters shared between early and late hatching treatments within time periods (*e.g.*, Eh T0 *vs.* Lh T0 etc.) are not statistically different at alpha > 0.05 (Tukey's HSD multiple comparison).

	Early Hatching treatments			Late Hatching treatments		
Period	T0	T1	T2	T0	T1	T2
Sedge						
in *C. mackenzeii*	27.1 ± 2.1 a	23.7 ± 2.2 a	18.33 ± 2.8 a	35.6 ± 2.7 b	25.6 ± 2.4 a	18.5 ± 3.4 a
in *C. ramenskii*	81.7 ± 10.7 a	75.9 ± 9.1 a	70.9 ± 11.6 a	105.2 ± 10.5 a	65.9 ± 8.7 a	79.0 ± 13.3 a
Grazing lawn						
without *T. palustris*	30.6 ± 4.0 a	39.5 ± 5.4 a	34.4 ± 5.8 a	32.5 ± 3.9 a	21.5 ± 3.7 a	36.9 ± 7.9 a

Table 1.4. Standing crop biomass offtake (g dwt. m^{-2} d^{-5}) for Cackling Canada gosling experiment. Data represent the mean ± 1 SE of *T. palustris* within *C. mackenzeii* and *C. ramenskii* dominated meadows and grazing lawns found in the upper Kashunuk River drainage. Letters shared within rows are not statistically different at alpha > 0.05 (Tukey's HSD multiple comparison).

	Early Hatching treatments		Late Hatching treatments	
	High availability	Low availability	High availability	Low availability
Triglochin palustris				
in *C. mackenzeii*	3.1 ± 0.6 a	0.2 ± 0.2 b	1.5 ± 0.7 ab	1.2 ± 0.4 b
in *C. ramenskii*	1.6 ± 1.0 a	- 0.9 ± 0.9 b	1.5 ± 1.1 a	-0.2 ± 0.5 b
in grazing lawn	5.0 ± 0.8 a	-0.3 ± 0.3 b	5.3 ± 0.49 a	0.3 ± 0.3 b
Sedge				
in *C. mackenzeii*	3.4 ± 2.8 ab	3.7 ± 2.0 ab	9.9 ± 3.4 a	-3.7 ± 3.1 b
in *C. ramenskii*	5.8 ± 8.4 ab	-3.2 ± 12.7 ab	39.3 ± 14.5 a	-27.5 ± 11.2 b
Grazing lawn	-8.9 ± 5.7 ab	4.0 ± 4.4 a	11.0 ± 4.8 a	-18.2 ± 6.7 b

Table 1.5. Environmental effects on Cackling Canada gosling growth. Treatments include effects of seasonal decline in the quality of foods and the effect of variation in availability of forage on gosling mass and structural characteristics. Results are from PROC Mixed model procedures with a correlation matrix modeled as an AR(1) process (SAS Institute Inc., 1990). We entered treatment, time, individual, and sex as class variables, and gosling age as a continuous variable. Treatment by age interactions were used to test for differences in mass and structural measurements.

	Type 3 Tests of Fixed Effects			
	Treatment	Sex	Time	Treatment * Age
Mass	$F_{3,25} = 3.7$; $P = 0.025$	$F_{1,866} = 2.4$; $P = 0.12$	$F_{1,866} = 6745$; $P < 0.0001$	$F_{3,866} = 80.5$; $P < 0.0001$
Tarsus	$F_{3,25} = 4.8$; $P = 0.0085$	$F_{1,296} = 9.7$; $P = 0.002$	$F_{1,296} = 6694$; $P < 0.0001$	$F_{3,296} = 54.9$; $P < 0.0001$
Head Length	$F_{3,25} = 7.9$; $P = 0.0007$	$F_{1,296} = 10.5$; $P = 0.001$	$F_{1,296} = 14347$; $P < 0.0001$	$F_{3,296} = 98.7$; $P < 0.0001$
Culmen	$F_{3,25} = 5.3$; $P = 0.0059$	$F_{1,296} = 7.9$; $P = 0.005$	$F_{1,296} = 3907$; $P < 0.0001$	$F_{3,296} = 45.6$; $P < 0.0001$
Ninth Primary	$F_{3,25} = 2.7$; $P = 0.066$	$F_{1,296} = 0.8$; $P = 0.37$	$F_{1,296} = 434$; $P < 0.0001$	$F_{3,296} = 16.3$; $P < 0.0001$

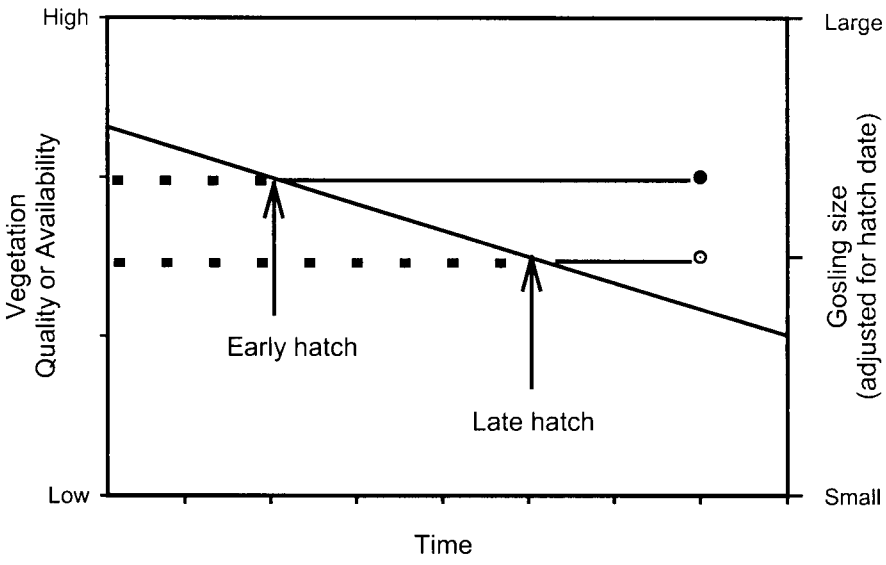

Figure 1.1. Schematic diagram of the hypotheses linking seasonal variation in forage quality and availability to variation in gosling size. Arrows indicate the variation in nitrogen content of vegetation available to early (EH) and late hatched (LH) goslings.

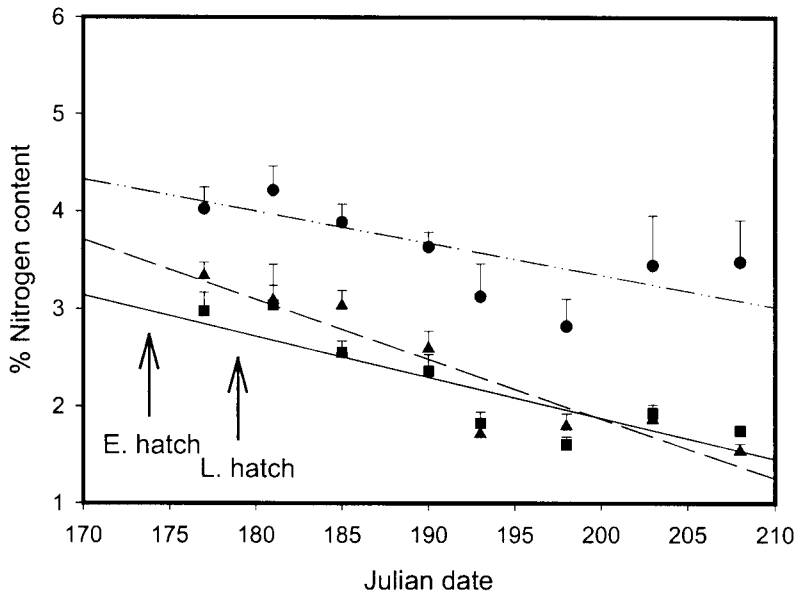

Figure 1.2. Seasonal decline in the nitrogen content of key forage species used by imprinted goslings. Arrows correspond to the six day variation in collection of early-hatched (EH) and late-hatched (LH) Cackling Canada goslings. Nitrogen content of forage species are represented by the symbols: (●) *Triglochin plaustris*, (▲) *Carex mackenzeii*, and (■) for *C. ramenskii*. Results from linear regression and line style are as follows: (— ··· —)*T. plaustris*: %N = 9.9 – (0.03 * day), r^2=0.28, P = 0.008; (----) *C. mackenzeii*: %N = 13.4 – (0.06 * day), r^2=0.42, $P < 0.0001$; and (——) *C. ramenskii*: %N = 11.2 – (0.05 * day), r^2=0.48, $P < 0.0001$.

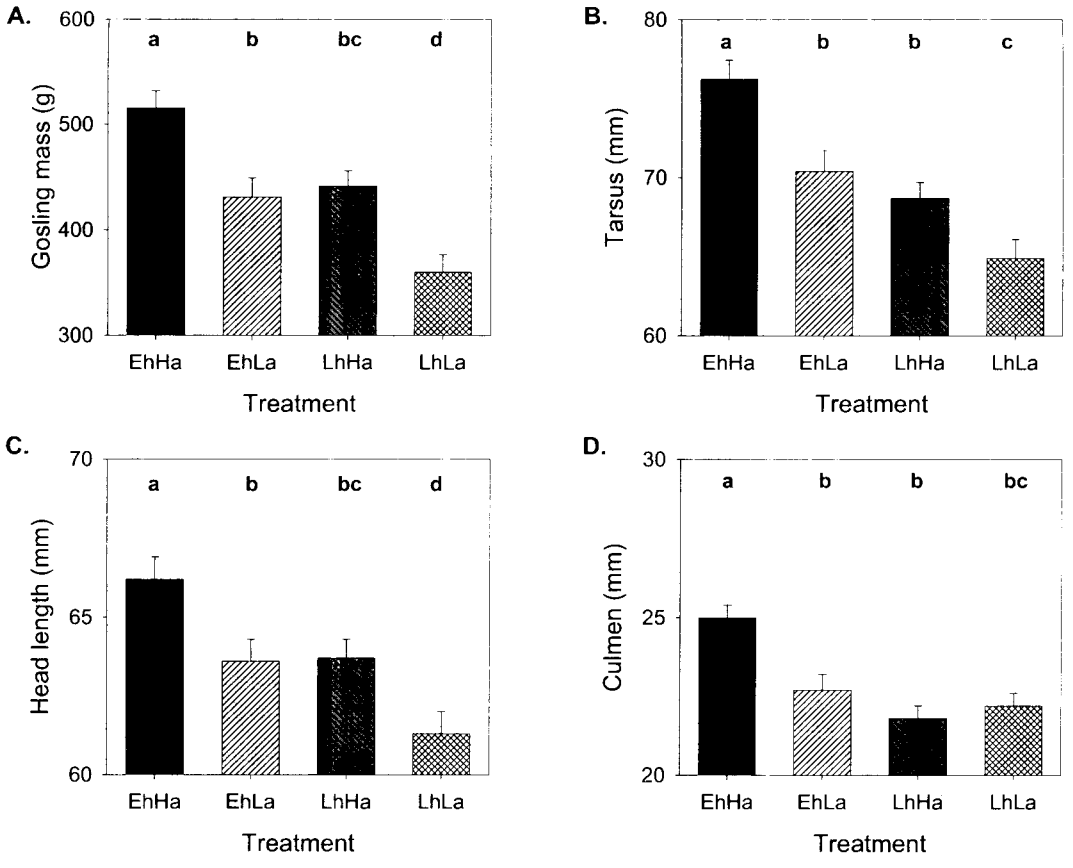

Figure 1.3. Experimental effects on: A.) mass, B.) tarsus, C.) head length, and D.) exposed culmen traits of 31 day old Cackling Canada goslings. Treatment codes and sample sizes are as follows: (EhHa) early-hatched high availability (n=7), (EhLa) early-hatched low availability (n=6), (LhHa) late-hatched high availability (n=9), and (LhLa) late-hatched low availability (n=8) goslings. Data represent least squared means (LS means) ± 1 SE after controlling for treatment, time, individual, and sex differences as class variables and gosling age as a continuous variable. Treatment by age interactions were used to test for differences in mass and structural traits (PROC Mixed). Letters represent within trait multiple comparisons (Tukey's HSD) among treatments if a significant treatment by age interaction was found at alpha < 0.05. Letters shared between treatment groups do not statistically differ at alpha < 0.05.

CHAPTER 2. Forage variation in brood-rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska[2]

Summary

1. We investigated the effects of grazing by black brant geese on *Carex subspathacea* lawns on the Yukon-Kuskokwim Delta, Alaska.

2. We compared variation in growth and forage quality in both grazed and temporarily exclosed sites to determine responses of *C. subspathacea* to grazing at landscape scales within two nesting colonies that had experienced different population dynamics over recent decades.

3. Landscapes differed in forage quality, grazing patterns, and in the effect grazing had on *C. subspathacea* forage characteristics. We found no effect of grazing on net above-ground primary productivity (*NAPP*) over a wide range of natural grazing intensities at the landscape scale.

4. No differences in forage quality, *NAPP*, or response of *C. subspathacea* growth rates to grazing pressures could be detected between colonies. This suggests that goose grazing does not have deleterious effects on *C. subspathacea* in this ecosystem.

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[2] Published as Person, B.T., Babcock, C.A., Ruess R.W. (1998) Forage variation in brood-rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska. *Journal of Ecology*, **86**, 243-259.

5. It has been suggested that gosling growth rates are sensitive to seasonal declines in forage availability and quality. Spatial variation in forage quality and availability per sampled area exceeded seasonal variation in these characteristics and is likely to have dramatic effects on gosling growth and recruitment rates.
Key-words: Sub Arctic, salt marsh, graminoids, grazing lawns, plant-animal interactions.

Introduction

Forage quality and abundance have substantial effects on secondary productivity and life history characteristics of geese (Sedinger *et al.* 1995a). Because geese are capable of dispersal to areas where their fitness may be higher, it is important to understand spatial variation in net above-ground primary productivity (*NAPP*), as well as the availability of forage, its quality, and the responses of vegetation to grazing pressure. Goose-grazing systems have been shown to be excellent models for studying the processes responsible for maintenance of grazing lawns (Bazely & Jefferies 1985; Kotanen & Jefferies 1987; Hik & Jefferies 1990), but few investigations have incorporated the spatial variability experienced by populations of breeding geese while rearing young (Gauthier *et al.* 1995). Most work on goose-grazing systems has been done on the relationship between both pure and mixed *Puccinellia phryganodes* (Trin.) Scribn. & Merr. / *Carex subspathacea* Wormsk. grazing lawns and lesser snow geese (*Anser caerulescens caerulescens* L.) in the eastern Canadian subarctic. These studies have shown that nutrients recycled through goose faeces are critical for the maintenance

of rapid plant growth in heavily grazed swards (Cargill & Jefferies 1984a; Bazely & Jefferies 1985; Ruess *et al.* 1989), and that intermediate levels of grazing by geese may increase *NAPP* relative to heavily grazed or ungrazed swards (Hik & Jefferies 1990). Further, grazing can increase the nitrogen content of above-ground biomass by shifting the demography of swards towards those containing younger and more mitotically active individuals (Bazely & Jefferies 1985; Kotanen & Jefferies 1987).

Along the coastal flats of the Yukon-Kuskokwim (Y-K) Delta in southwestern Alaska, pacific black brant (*Branta bernicla nigricans* Lawrence) maintain grazing lawns of *C. subspathacea*. Brant spend a disproportionate amount of time feeding on these lawns relative to their availability (Lang & Raveling 1993; Sedinger 1995b). Geese with goslings forage almost exclusively on *C. subspathacea* lawns in the period immediately following hatch. During this time, goslings are most sensitive to the availability and quality of forage. Late hatching brant goslings have reduced growth rates (Sedinger & Flint 1991) and smaller goslings have lower survival and recruitment rates (Sedinger *et al.* 1995a). It has been suggested that seasonal decreases in gosling growth rates reflect seasonal declines in nitrogen content and availability of forage throughout the brood rearing period, coupled with constraints on intake rate due to low gut volumes (Sedinger & Raveling 1988; Cooch *et al.* 1991; Sedinger and Flint 1991; Lindholm *et al.* 1994; Sedinger *et al.* 1997).

Colonies of black brant that nest on the Y-K Delta have undergone dramatic demographic changes in recent decades. For instance, the Tutakoke River colony decreased from an estimated 7400 to 1100 breeding pairs between 1981 and 1986

(Sedinger *et al.* 1993), but has since increased to an estimated 5596 (R. Michael Anthony unpublished data for 1995). One colony on the Y-K Delta (Kokechik Bay) has however remained stable between 1981 and 1995 with an average population of 6955 ± 744 (Sedinger *et al.* 1993; R. Michael Anthony unpublished data). The contrast in demographic patterns between these two colonies allowed us to compare *C. subspathacea* grazing lawns that had experienced historically dissimilar grazing patterns.

We characterized variation in growth and forage quality responses of *C. subspathacea* to grazing at landscape scales within two brant colonies. We also investigated spatial variation in grazing patterns within and between goose colonies. These questions are relevant to the grazing ecology of this system because there is considerable variation in climate, geomorphology, flooding and sedimentation disturbance, and historic distributions of geese throughout the distribution of the *C. subspathacea* community (Christopher A. Babcock unpublished data). Because geese show among-year fidelity to distinct brood rearing areas within a colony (Mark S. Lindberg unpublished data), it is conceivable that spatial variation in the dynamics of these grazing lawns could have life history consequences for geese.

In order to test these ideas, we employed a novel experimental approach, in which a movable exclosure was used to investigate the interaction between the effects of grazing and growth and nutritional value of *C. subspathacea* both within and between successive time periods. We focused on plant-herbivore processes that occurred at spatial and temporal scales relevant to brant colony demography. Plant responses to grazing were therefore followed over the period when goslings were most sensitive to

forage availability and quality (Cooch *et al.* 1991; Sedinger and Flint 1991; Cooch *et al.* 1993; Sedinger *et al.* 1997).

Methods

STUDY AREA

The Yukon-Kuskokwim Delta is a large expanse of coastal saltmarsh in the near Arctic. Primary productivity supports several populations of breeding waterfowl which in turn are an important source of protein in the subsistence-based economy of the Yupik peoples of this area (Klein 1966).

The *C. subspathacea* community is discontinuously distributed along the interface between coastal, riparian and ephemeral pond margins and the slightly more elevated *Carex ramenskii* Kom. meadow community (Kincheloe & Stehn 1991). *Carex subspathacea* occurs both in bands less than 10 cm wide around mud-islands, and in swards up to 0.25 km^2 on the Y-K Delta. The *C. subspathacea* community is a nearly homogeneous grazing lawn which also contains < 10% of mixtures of *Puccinellia phryganodes* and *Potentilla egdeii* Wormsk. (Kincheloe & Stehn 1991). Black brant prefer this community and their grazing maintains a short (0.25 - 1.5 cm) canopy. Tidal waters inundate the community several times per month with waters ranging in salinity from 25 to 3.5 g solute per litre depending on distance from the Bering Sea (Christopher A. Babcock, unpublished data).

EXPERIMENTAL DESIGN

We designed a three-sided exclosure with a movable fence so that wild geese could graze passively at natural intensities within the open portion (Fig. 1). In the growing seasons of both 1994 and 1995, the diagonal fence was moved 21 days after initial harvest (Fig. 1). In 1995 the design was expanded by fencing along the fourth side of the exclosure 42 days after initial harvest. We were therefore able to harvest from plots that were grazed / open (O) or exclosed for the first 21 days (X); grazed for 42 days (OO) or exclosed for 42 days (XX), grazed for the first 21 days and subsequently exclosed for 21 days (OX) or exclosed for the first 21 days and then grazed for 21 days (XO); and in 1995 grazed for 54 days (OOO) or subsequently exclosed for 14 days (OOX). The sampling schedule differed slightly between years and location (Table 1). This design yielded data comparable to that of a movable exclosure type experiment. We define plots that always experienced grazing to be control plots because this plant community always experiences grazing during the growing season.

In 1994 ten replicate exclosures were established at each of four landscape positions in the Tutakoke colony area, hereafter referred to as the Kashunuk drainage (Fig. 2): Tutakoke (TU), Lower Kashunuk (LK), Onumtuk Bend (OB), and Emperor Bend (EB). This design was repeated in 1995 and expanded to include two landscape positions in the Kokechik Bay area: Kokechik West (KW), and Kolomak River (KO) landscapes (Fig. 2). Brant colonies are centred on the Tutakoke and Kokechik West sites. Post hatch, core colonies are used as brood rearing sites by groups of brant. Seven to 14 days following river ice break-up, replicate exclosures were distributed across a 1-2 km

distance within each landscape on various coastal, riparian, and ephemeral pond margin swards dominated by *C. subspathacea*. Landscapes were chosen on the basis of their accessibility by skiff or float plane and were separated by approximately 10 km. Landscapes differed in proximity to the core colonies, salinity of tidal waters, and edaphic characteristics (Christopher A. Babcock, unpublished data). Landscapes in the Kashunuk drainage have been shown to represent distinct brood rearing areas to which individual brant show year-by-year fidelity (Mark S. Lindberg, unpublished data).

SAMPLING AND VEGETATION ANALYSIS

One 10 x 10 cm turf was removed at the time the exclosures were erected and from each of the treatments within the exclosures at the end of the appropriate sampling period (Table 1). All above-ground biomass was clipped to ground surface from each turf within 24 hr of harvest, washed in fresh water, and dried at 60^{o} C in a field laboratory (Bazely & Jefferies 1985). Vegetation was then redried and weighed ± 0.001 g at the University of Alaska, Fairbanks. In 1995, three of 40 samples from the Kokechik West landscape could not be taken at the end of the second period because two exclosures were damaged by driftwood on a flood tide. Stem density was measured in 1995 by placing a 9.5 cm^2 quadrat in the centre of each turf and counting the number of basal meristems within the area. Stem density was not measured for the initial harvest.

All above-ground biomass was ground in a 20 mesh size Wiley Mill and combusted in a LECO CNS 2000 autoanalyzer (Michigan, USA) for determination of

nitrogen and carbon content. One sample from a plot which had been grazed for 21 days at the Tutakoke River landscape in 1995 did not have enough biomass for nitrogen determination.

In 1995 we established four plots, separate from our grazing experiment, throughout the Tutakoke River landscape to estimate more precisely the seasonal changes in the quality of pure stands of *C. subspathacea*. Plots were sampled within 1 week of snow melt and subsequently sampled every 14 ± 3 days. We clipped all above-ground biomass from 30 x 30 cm turves and processed live biomass as described above. Ground samples were analyzed for percent ash, and acid (ADF) and neutral detergent fibre (NDF) content using the Van Soest method (Goering & Van Soest 1970).

STATISTICAL ANALYSIS

Measurements

Net above-ground primary productivity (*NAPP*) of grazed swards was estimated as the difference between biomass present after we exclose and the biomass of the previous grazed sward, divided by the number of days exclosed (see McNaughton *et al.* 1996 for discussion). Estimates of *NAPP* were therefore calculated for each replicate over two and three successive time periods in 1994 and 1995, respectively, using the following formulae:

1). Period 1 *NAPP*: (X biomass - T0 biomass) ÷ days exclosed

2). Period 2 *NAPP*: (OX biomass - O biomass) ÷ days exclosed

3). Period 3 *NAPP*: (OOX biomass - OO biomass) ÷ days exclosed

We include negative estimates of *NAPP* because eliminating them would overestimate *NAPP*. We estimate *NAPP* of an ungrazed sward (X*NAPP*) to be the increase over time of a continuously exclosed sward (*i.e.*, (XX - X) divided by interval days. Apparent offtake was estimated as the difference between above-ground biomass between exclosed plots and plots that experienced grazing pressure during the corresponding interval. As for *NAPP*, apparent offtake was estimated over two and three successive time periods in 1994 and 1995, respectively. We define offtake as 'apparent offtake' because one of the hypotheses in this experiment is that grazing influences the rate of growth of the vegetation. Caution should be taken when these estimates are used in nutritional models because *NAPP* may be affected by grazing, thus apparent offtake may over- or under-estimate true offtake. As with *NAPP*, we included all positive and negative estimates of apparent offtake. We estimated the amount of *NAPP* consumed by summing apparent offtake across periods divided by interval days. Percent of annual *NAPP* consumed is the ratio of apparent consumption and *NAPP* multiplied by 100%.

We used standing crop biomass of grazed (control) plots throughout the season as an index of grazing intensity. Faeces counts were a poor index of use by geese due to wind rolling and tidal inundation. Use of standing crop biomass as an estimate of grazing pressure is not new (Hik *et al.* 1991) and we used it to describe differences in grazing patterns among years and landscapes. Although our design lends itself to the use of a published formula for grazing intensity (McNaughton 1979), this derived index of grazing intensity could be statistically autocorrelated with *NAPP* (Mitchell & Wass 1996).

Statistical procedures

We analyzed overall treatment variation in: standing crop biomass, nitrogen content, standing crop nitrogen (SCN), and the carbon to nitrogen ratio (C:N) of *C. subspathacea* based on a nested ANOVA. We entered colony, landscapes nested within colony, exclosure and treatment as fixed variables and included landscape x treatment interactions. Colony effects were tested using F= colony MSE divided by the MSE of landscape nested within colony. We entered exclosure as a fixed variable to control for within exclosure variation and tested treatment effects using F = treatment MSE divided by exclosure MSE. Analyses were performed on each year and colony separately because treatments and number of colonies varied between years. The approach ensured that all analyses were balanced below the landscape level. We performed linear contrasts between treatments when a significant treatment effect was found. In order to control for within exclosure variation, exclosure MSE was included in the denominator of F tests of linear contrasts.

We compared differences in control plots between colonies and among landscapes in the following response variables: *NAPP*, apparent offtake, stem densities, nitrogen content, SCN, and the C:N of *C. subspathacea*. We tested for colony differences using a nested ANOVA and entered colony, and landscapes nested within colony as fixed variables and included landscape x treatment interactions. Colony effects were tested using F= colony MSE divided by the MSE of landscape nested within colony. We did not enter exclosure as a factor in these analyses because only one sample from each of ten exclosures within each landscape were used to test for within colony variation. Analyses

of landscape variation was performed on separate years and colonies, even when no significant year or colony effect was detected. We approached the analysis this way because geese show fidelity to nesting and brood-rearing sites within colonies and because our sampling protocol differed slightly between years. If a significant landscape effect was found, further analysis of landscape differences were determined using Tukey's HSD multiple comparison.

Colony and landscape variation in grazing intensity (standing crop biomass of grazed plots) was analyzed using ANCOVA. Low standing crop biomass could have resulted either from low rates of productivity, high amounts of bare ground, or high grazing intensity. To partition variation associated with productivity and amounts of bare ground we entered *NAPP* and stem density as covariates and tested for differences in grazing intensity between colonies and among landscapes. Colony variation was determined using tests previously described. As with control plot variation in *NAPP*, apparent offtake, and nutritional characteristics, analyses were performed on separate years and colonies to determine landscape differences in grazing intensity. Tukey's HSD multiple comparisons were performed when a significant landscape effect was found.

We used ANOVA based on a repeated measures design to test for seasonal changes in control plots. Year effects in all analyses were determined by including only treatments that were applied in each year of the study in order to maintain a balanced design. We used a repeated measures ANOVA to test for seasonal changes in percent ash, and ADF and NDF of *C. subspathacea* collected in plots established for this purpose.

We used ANCOVA to partition variation associated with the production of vegetation which had been grazed in the previous time period (OX biomass). Net above-ground primary production of swards exclosed for 42 days (X*NAPP*), and biomass grazed for 21 days (O biomass) were covariates; colony and landscape position within colony were entered as a fixed variables. We included the interaction between *NAPP* of exclosed swards and colony, and the interaction between colony and biomass grazed for 21 days. These interactions allowed us to control for variation in the inherent productivity between colonies (X*NAPP* x colony), and to distinguish the effect grazing had on subsequent production from the dependency of production on beginning biomass (O biomass x colony). We believe this is an appropriate approach for determining variation in growth patterns following natural grazing pressures. *A priori* tests for differences between *NAPP* of ungrazed and previously grazed swards at the landscape level were made using linear contrasts. This allowed us to determine whether grazing pressures had an effect on subsequent *NAPP*. All data met model assumptions of normality and homogeneity of variance. Analyses were performed using General Linear Models procedures, using SAS Institute software (1990).

Results

COLONY DIFFERENCES

We found no overall differences in *NAPP*, grazing intensity, apparent offtake, stem densities, nitrogen content of *C. subspathacea* swards, SCN, or the C:N between the Kokechik Bay and Tutakoke colonies at any period of the growing season. All overall

nested ANOVA models used to test for differences in these response variables had $F_{1,4}$ values < 3.46, $P > 0.06$. There were, however, trends whose ecological interest is discussed later.

LANDSCAPE EFFECTS

Net aboveground primary productivity

Net above-ground primary productivity of grazed plots did not differ among Kashunuk drainage landscapes in 1994 (early-season overall $F_{3,36} = 1.28$, $P = 0.29$; mid-season overall $F_{3,36} = 1.36$, $P = 0.27$). In 1995, *NAPP* differed among landscapes during the early- and mid-growing season (early-season overall $F_{3,36} = 2.97$, $P = 0.045$; mid-season overall $F_{3,36} = 3.18$, $P = 0.035$). We detected no differences in *NAPP* between landscapes in the Kokechik Bay colony. The Emperor Bend and Lower Kashunuk landscapes generally had the highest productivity throughout both growing seasons (Table 2). Late-season *NAPP* at Emperor Bend was nearly 10 times higher than the next most productive landscape in the Kashunuk drainage in 1995. Early-season *NAPP* at the Tutakoke landscape was 10% higher in 1995 than in 1994 (year effect $F_{1,3} = 15.58$, $P = 0.0002$). Net above-ground primary productivity declined throughout the summer of 1995 at the Kashunuk drainage landscapes (overall $F_{2,35} = 35.57$, $P < 0.0001$) from 1.98 g m^{-2} d^{-1} to 0.19 g m^{-2} d^{-1}, while it remained nearly constant throughout the season at the Kokechik Bay colony landscapes (Table 2).

Differences in grazing intensity, apparent offtake, and consumption among landscapes

Grazing intensity, as indexed by standing crop biomass in grazed plots, differed initially within the Kokechik Bay landscapes (overall model $F_{1,18} = 11.10$, $P = 0.0037$); the Kolomak River had 60% lower grazing intensity than the Kokechik West landscape (Table 3). No further differences in grazing intensity could be detected between Kokechik Bay landscapes at any period in the season. Grazing intensity at the Kokechik Bay landscapes did not differ throughout the season (ANOVA based on a repeated measures design $F_{3,14} = 1.88$, $P = 0.18$).

Grazing pressures differed among landscapes within the Kashunuk drainage at all time periods during both years of the study (Table 3). We found seasonal variation in grazing intensity among landscapes in the Kashunuk drainage in both 1994 (ANOVA based on a repeated measures design $F_{3,36} = 39.9$, $P < 0.0001$), and 1995 (ANOVA based on a repeated measures design $F_{3,36} = 33.6$, $P < 0.0001$).

We found between year variation in grazing intensity at the time of initial harvest (year effect $F_{1,75} = 20.04$, $P < 0.0001$), and in plots grazed for approximately 42 days (year effect $F_{1,75} = 5.66$, $P = 0.019$). Mid-season grazing intensity was 46 % higher in 1995 when averaged across all landscapes in the Kashunuk drainage. In 1994 the Tutakoke landscape sustained the highest grazing intensity throughout the season. When compared to the Onumtuk Bend landscape, which consistently experienced the next highest grazing pressure, grazing intensity was 98% higher at Tutakoke when averaged across the 1994 season. Similarly, in 1995 the Tutakoke and Onumtuk Bend landscapes

tended to experience the highest grazing intensities. Tutakoke had a seasonal average of 16.4 g m^{-2} standing biomass in 1994 compared to a seasonal average of 24.9 g m^{-2} standing biomass in 1995. In contrast, Emperor Bend had the lowest grazing intensity throughout 1994 and 1995 having a seasonal average of 65.2 and 43.3 g m^{-2} standing crop biomass in grazed plots, respectively.

Removal of goose grazing resulted in increases in standing crop biomass regardless of year, period of season, colony, or landscape position (Table 3). Averaged across all landscapes within each colony, biomass in plots exclosed for 42 days was 27% greater in the Kashunuk drainage when compared to Kokechik Bay.

Geese consumed 93% of the *NAPP* in the Kashunuk drainage landscapes between mid June and late July in 1994. Consumption was higher in 1995 when geese consumed 99% of the *NAPP* between June 7 and August 2. Ninety-five percent of above-ground production was consumed in Kokechik Bay between June 10 and August 2 in 1995.

Apparent offtake did not differ among landscapes in the Kashunuk drainage in 1994 (Table 4). In 1995, we found differences in apparent offtake among landscapes among the Kashunuk drainage landscapes during the mid- and late-periods of the growing season (Table 4). Apparent offtake did not differ between years ($F_{1,79} = 0.58$, $P = 0.44$).

Effects of grazing on plant growth

Our model used to partition effects of early-season grazing on production of above-ground biomass (OX biomass) explained a significant amount of the variance in

OX biomass ($F_{9,57} = 4.49$, $P = 0.0003$; $r^2 = 0.45$). We found no overall colony effect (ANCOVA $F_{1,57} = 0.05$, $P = 0.83$), but landscapes within colonies varied in the production of OX biomass (ANCOVA $F_{4,57} = 3.93$, $P = 0.0078$). We detected a significant colony x exclosed *NAPP* interaction (ANCOVA $F_{1,57} = 4.41$, $P = 0.041$) resulting from lower exclosed *NAPP* in the Kokechik Bay area than in the Kashunuk drainage. Starting biomass (O biomass) did not explain a significant amount of the variance in this model (ANCOVA $F_{1,57} = 3.01$, $P = 0.089$), nor was there a significant interaction between O biomass and colony (ANCOVA $F_{1,57} = 0.12$, $P = 0.73$). The latter result suggested that grazing had no effect on the production of above-ground biomass because starting biomass (O biomass) had the same effect within each colony. If this interaction had been significant it would have suggested that variation in the production of OX biomass would have been associated not just with starting biomass, but the inherent effect of grazing pressures at the colony scale.

We further investigated the effects of grazing on plant growth at the landscape scale by performing linear contrasts between exclosed *NAPP* and the *NAPP* of swards that experienced grazing early in the season. We found no effect of grazing on *NAPP* at any landscape in either 1994 or 1995 (Linear contrast, $P > 0.15$)(Fig. 3). Had early-season grazing pressures effected *NAPP* positively we would have expected to see lower *NAPP* of vegetation exclosed for 42 days.

Stem densities in grazed plots differed between landscapes at Kokechik Bay early in the season, when stem density was highest at the Kolomak River landscape (overall

$F_{1,17} = 8.30$, $P = 0.01$). We found landscape variation in stem densities among grazed plots for all periods of the season within the Kashunuk drainage (early-season $F_{3,34} = 9.17$, $P < 0.0001$; mid-season $F_{3,35} = 4.34$, $P = 0.01$; late-season $F_{3,35} = 6.13$, $P = 0.0018$). Averaged across the season, the Tutakoke and Emperor Bend sites had the highest stem densities in grazed plots (26283 ± 2361 SE, 22895 ± 1950 SE, stems m^{-2}, respectively).

NUTRITIONAL CHARACTERISTICS

Nitrogen content of grazed and exclosed Carex subspathacea

Landscapes within both colonies tended not to differ in the nitrogen concentration of grazed swards (Table 5), although vegetation in the Lower Kashunuk landscape consistently had lower nitrogen than other landscapes in the Kashunuk drainage in both 1994 and 1995 (Table 5). Averaged across the season, grazed swards in the Lower Kashunuk landscape had 2.9 and 3.5 % nitrogen in 1994 and 1995, respectively. We found both annual and seasonal variation in the nitrogen content of grazed swards. In 1995, initial nitrogen content of *C. subspathacea* was 17% higher than 1994 when averaged across all landscapes within the Kashunuk drainage (year effect $F_{1,75} = 33.13$, $P < 0.0001$). Similarly, nitrogen content of vegetation grazed for approximately 21 days was higher in 1995 relative to 1994 (year effect $F_{1,75} = 5.99$, $P = 0.016$) (Table 5). In 1995 there was a 10 % increase in the nitrogen concentration of grazed swards between late July and early August resulting in a nitrogen content of *C. subspathacea* that was

similar to values observed in late June. This late-season trend was observed in both grazed and exclosed plots (Table 5).

We found significant variation in the nitrogen concentration of *C. subspathacea* between treatments in both years of the study (1994 treatment effects $F_{3,36} = 12.65$, $P < 0.0001$; 1995 $F_{3,36} = 20.35$, $P < 0.0001$)) and at each colony (Kokechik Bay treatment effects $F_{1,18} = 6.9$, $P = 0.017$) (Table 5). We found annual variation in nitrogen concentration of *C. subspathacea* swards following the removal of grazing pressure (year effect $F_{1,36} = 6.13$, $P < 0.018$). The nitrogen content of 21 day exclosed swards tended not to differ from grazed swards in 1994, while grazed swards tended to have 10 % higher nitrogen values in 1995 (Table 5).

Standing crop nitrogen is the product of nitrogen concentration and standing crop biomass and we refer to SCN in grazed plots as 'available nitrogen'. We found variation in available nitrogen among landscapes within the Kashunuk drainage at all periods of the season in both 1994 and 1995 (Table 6). At all time periods in 1994 and 1995, Emperor Bend had approximately twice the available nitrogen when compared to all other Kashunuk landscapes (Table 6). Landscapes in the Kokechik Bay colony differed in available nitrogen at the time of initial harvest (ANOVA $F_{1.18} = 4.67$, $P = 0.0444$), and in late June ($F_{1.17} = 4.93$, $P = 0.0403$). Kokechik West had 32% more available nitrogen than did the Kolomak River landscape during the initial harvest. In contrast, the Kolomak River site had 50% more available nitrogen at the time of hatch in late June (Table 6). We found seasonal declines in available nitrogen in 1994 (repeated measures

ANOVA time effect $F_{2,35} = 8.89$, $P = 0.0008$) and 1995 (time effect $F_{3,34} = 20.79$, $P < 0.0001$) in the Kashunuk drainage. No significant seasonal variation in available nitrogen could be detected between Kokechik Bay landscapes (time effect $F_{3,14} = 2.75$, $P = 0.082$) (Table 6).

Removal of grazing pressure from *C. subspathacea* swards had a significant overall effect on SCN in the Kashunuk river drainage (1994 treatment effect $F_{3,36} = 7.67$, $P < 0.0001$;1995 treatment effect $F_{3,36} = 21.87$, $P < 0.0001$), and within Kokechik Bay landscapes (treatment effect $F_{1,18} = 8.67$, $P = 0.019$. Excluding geese from *C. subspathacea* swards resulted in greater SCN in all landscapes at Kokechik Bay (Table 6). This pattern was not as consistent among landscapes in the Kashunuk drainage and treatment effects on SCN differed among landscapes within the Kashunuk drainage in both 1994 and 1995 (1994 location x treatment $F_{18,36} = 2.60$, $P = 0.0152$; 1995 location x treatment $F_{24,36} = 4.013$, $P < 0.0001$). The Lower Kashunuk landscape was the most consistent exception; in this landscape SCN tended not to differ between exclosed and grazed vegetation in either 1994 or 1995 (Table 6).

Fibre analysis

We detected no seasonal effects in % ash (repeated measures ANOVA $F_{4,11} = 1.76$, $P = 0.23$), NDF ($F_{4,11} = 1.99$, $P = 0.26$), or ADF ($F_{4,11} = 3.14$, $P = 0.078$) in *C. subspathacea* collected throughout the growing season at the Tutakoke landscape. Overall mean values are; % ash (14.1 ± 0.5%), NDF (52.2 ± 0.2), and ADF (19.9 ± 0.4).

One replicate was removed from statistical analysis due to contamination by soil (% ash was 2 times greater than all other ash values).

Carbon to nitrogen ratio of grazed and exclosed swards

Carbon to nitrogen ratio (C:N) is the ratio of carbon to nitrogen content of all above-ground biomass and we use this as an index of nutritional quality of *C. subspathacea* swards. We consider vegetation with high C:N ratio to be poorer quality forage for brant. In both 1994 and 1995 we found landscape variation in C:N of grazed swards within both colonies and at all periods of the season except in August of 1995 (Table 7). The Lower Kashunuk site consistently had higher C:N than all other Kashunuk drainage landscapes (Table 7). Averaged throughout the growing season, C:N in grazed swards in the Lower Kashunuk were 15.8 and 12.6 in 1994 and 1995, respectively. Landscapes within the Kashunuk drainage with the next highest C:N of grazed swards were Emperor Bend (11.7) in 1994, and Tutakoke (11.5) in 1995. Within the Kokechik Bay colony, the Kokechik West landscape had a higher C:N than did the Kolomak River landscape until late season, at which time C:N of the grazed plots did not differ (Table 7). A seasonal increase of the C:N was observed at both colonies (1994 overall effect of time $F_{2,32} = 40.5$, $P < 0.0001$; Kashunuk drainage 1995 overall effect of time $F_{3,32} = 38.3$, $P < 0.0001$; Kokechik Bay overall effect of time $F_{3,14} = 8.99$, $P = 0.0014$), and in both 1994 and 1995. Carbon to nitrogen ratios increased throughout the season at all landscapes within each colony (Table 7).

Removal of grazing pressure increased C:N ratios within the Kashunuk drainage (1994 treatment effect $F_{6,36}$ =16.22, $P < 0.0001$; 1995 treatment effect $F_{6,36}$ =11.98, $P < 0.0001$) and Kokechik Bay landscapes (treatment effect $F_{8,18} = 8.97$, $P = 0.0078$), although there were significant location by treatment interactions within the Kashunuk drainage in 1995 (Table 7). The latter is of interest because removal of grazing pressures did not affect the C:N in the same way at all landscapes. The most notable exceptions were the Lower Kashunuk and Tutakoke landscapes where grazing tended not to decrease C:N.

Discussion

NET ABOVE-GROUND PRIMARY PRODUCTIVITY

There was a tendency for landscapes at Kokechik Bay to have less seasonal variation in rates of *NAPP* compared with sites in the Kashunuk drainage. We believe this is of ecological interest because late season *NAPP* of grazed swards throughout Kokechik Bay was nearly 5 times greater than *NAPP* in the Kashunuk drainage, although this difference was not significant. Our inability to detect colony differences in late season *NAPP* was affected by high rates of *NAPP* at the Emperor Bend landscape, relative to all other Kashunuk drainage landscapes, and this increased within colony variance. Several mechanisms could be responsible for higher rates of late-season *NAPP* in the Kokechik Bay landscapes. Salinity of water inundating the Kokechik Bay area may be lower than that of tidal waters in the Kashunuk drainage due to a spit at the mouth of Kokechik Bay reducing tidal exchange with the Bering sea. Decreased tidal exchange,

combined with freshwater run-off from the Askinuk Mountains at the north shore of Kokechik Bay is likely to reduce the salinity of Kokechik Bay. Srivastava & Jefferies (1995) reported a decrease in leaf births in *C. subspathacea* following high salinity treatments. It is plausible that the effect of interactions between salinity and grazing pressures may be manifested in decreased late season *NAPP* of *C. subspathacea* swards. Late season rates of *NAPP* at Emperor Bend do not conflict with the hypothesis outlined above. Emperor Bend is the most freshwater site on the Kashunuk drainage, and consistently experienced the lowest grazing pressures. Following a growing season of chronic exposure to salinity and grazing stresses, the trade-off between translocating belowground reserves for the production of above-ground tissues (Beaulieu *et al.* 1996), may not benefit *C. subspathacea* at a period of the season when photoperiod is decreasing. Rather, plants in areas that experienced both high salinity and grazing stresses throughout the season may shift allocation patterns at this time of the season and increase belowground reserves earlier than swards that did not experience high salinity and grazing stresses (Maschinski & Whitham 1989; Hik & Jefferies 1990; Hik *et al.* 1991; Srivastava & Jefferies 1995).

EFFECTS OF GRAZING ON *NAPP*

Early-season grazing had no effect on *NAPP* of *C. subspathacea* swards at any scale we tested. All linear contrasts used to test for landscape differences between grazed and exclosed *NAPP* had P values > 0.15 (Fig. 3). Our finding that grazing did not result in either over- or under-compensation of above-ground tissue is consistent with other studies of goose-grazing systems (Zellmer *et al.* 1993, Gauthier *et al.* 1995, Beaulieu *et*

al. 1996), but contrasts with work done on *C. subspathacea* at La Perouse Bay (Cargill & Jefferies 1984a). Seasonal grazing pressures averaged across both colonies in 1995 were 65% higher than those observed at La Perouse Bay. This comparison is based on average seasonal standing crop biomass estimates of *C. subspathacea* dominated swards reported by Cargill & Jefferies (1984a). These differences may reflect greater foraging efficiency of black brant compared to lesser snow geese, and grazing intensities on the Y-K Delta may be too severe for grazing to have a positive effect on *C. subspathacea NAPP*. Nonetheless, because of the wide variation in grazing intensities among landscapes, we predicted that *C. subspathacea* would respond either positively or negatively at one or more landscapes.

There are several possible explanations for our observation that grazing had no effect on *NAPP*. Nitrogen deposition has been demonstrated to increase productivity in ungrazed swards of *C. subspathacea* and *P. phryganodes* (Cargill & Jefferies 1984b ; Hik *et al.* 1991). We did not observe faeces in exclosed plots, but it is conceivable that exclosed plots received faecal nitrogen input via surface run-off and tidal waters, thus increasing exclosed *NAPP*. A second explanation for a lack of a difference in *NAPP* between grazed and exclosed plots may have resulted from our sampling protocol. We compared grazed and exclosed *NAPP* over an approximate 21 day interval. This period may have been too short for an effect of grazing to be manifested in *NAPP*. Beaulieu *et al.* (1996) found reductions in belowground soluble carbohydrates following herbivory. Production of tissues following herbivory has been shown to be dependent on belowground soluble carbohydrates, and the rate at which this occurs in *C. subspathacea*

swards may require a longer sampling interval than we practiced. Hik & Jefferies (1990) reported increases in *NAPP* that began to emerge after just 24 days re-growth yet the greatest differences were observed 36 and 48 days after grazing bouts in late June. Had we maintained and sampled our exclosed plots for an additional 14 to 21 days we might have observed a promotive effect in the *NAPP* of *C. subspathacea* swards. Nonetheless, if a promotive effect on *NAPP* requires more than 21 days to be manifested in this ecosystem, the response would be insignificant for consumers within the season. Our sampling protocol was designed to test these effects over a time scale and period of the season when goslings are most sensitive to the availability and nutritional quality of *C. subspathacea* (Sedinger and Flint 1991). As such, our findings demonstrate that brant are not able to benefit from increased *NAPP* following early season grazing pressures. This finding is significant because our experiment examines the response of *NAPP* to grazing pressure over a wide range of natural grazing intensities. Further, our study addresses this response at spatial scales that encompass variation in growth characteristics of *C. subspathacea* experienced by breeding populations of geese.

VARIATION IN GRAZING INTENSITY

We found significant inter-annual, and seasonal variation in grazing intensity experienced by *C. subspathacea* swards among landscapes within the Kashunuk drainage. Inter-annual variation was influenced by lower than average nesting success of half the Tutakoke colony in 1994 due to high nest predation by arctic foxes (*Alopex lagopus* L.). Nest predation in 1994 freed many geese from the feeding constraints of incubation. This resulted in early-season grazing pressures, indexed by standing crop

biomass, at the Tutakoke River landscape that were 214% higher than in 1995 during the period when geese would normally be spending the majority of their time incubating eggs (Eichholz 1996). Over the 1994 season, apparent offtake at the Tutakoke site was 75% greater than the Emperor Bend landscape which had the next highest seasonal apparent offtake of 13.7 g m^{-2}. Non- and failed-breeders typically leave the Y-K Delta in mid to late June, and migrate to moulting areas on the north slope of Alaska (Derksen *et al.* 1982). An increase in failed-breeders departing from the Kashunuk drainage in 1994 likely explains the reduction in grazing pressure during the brood rearing period.

Following hatch, grazing pressure increases two- to three-fold with the introduction of goslings, nonetheless, we did not detect a significant decline in standing crop biomass between our post hatch sample and late July (Table 3). Two possibilities exist for our inability to detect a decrease in standing crop biomass over this period. Peak hatch at the Tutakoke colony was on June 20 and June 16 in 1994 and 1995, respectively (James S. Sedinger unpublished data) and our index of grazing intensity following hatch therefore included both grazing pressures exerted by non- and failed breeders before peak hatch, and approximately 2 weeks of grazing by broods. Second, declines in grazing intensity, relative to greater *per capita* intake demand in late July, may in part reflect a change in habitat use in mid- to late July and stresses the importance of a better understanding of the use of other forage communities (Mulder *et al.* 1996; Ruess *et al.* 1997).

NUTRITIONAL CHARACTERISTICS OF *CAREX SUBSPATHACEA* SWARDS

We observed both seasonal and landscape variation in nitrogen content, as well as quality and availability of nitrogen of *C. subspathacea* in both years of the study. Seasonal declines in nitrogen content have been reported in other goose grazing systems (Gadallah & Jefferies 1995). Seasonal increases in C:N ratio result from a dilution of the vegetation nitrogen content relative to carbon content. We found that increases in C:N ratio did not occur from a seasonal increase in the fibre content of *C. subspathacea* because the percent ADF and NDF did not change throughout the season. Therefore, seasonal dilution of nitrogen is due to increased pools of non-structural carbohydrates. Grazing tended to ameliorate seasonal trends in nitrogen content and C:N by maintaining the short stature grazing lawns. Standing crop nitrogen declined throughout both years of the study. Hence, despite observing a slight increase in standing crop biomass early in the brood rearing season (Table 3), the availability of nitrogen declined throughout the season. Reductions in SCN are consistent with reports that broods both spend more time foraging, and have a greater *per capita* intake demand as the brood rearing season progresses and supports the hypothesis that reduced gosling growth rates are associated with a decline in the availability of forage (Sedinger *et al.* 1995a; Sedinger *et al.* 1997).

Seasonal and landscape variation in grazing patterns are of particular interest to us. We found significant variation in both the quality and availability of forage per sampled area among landscapes within both colonies. These differences were most marked in the Kashunuk drainage. A discrepancy exists between patterns of landscape use by black brant and the nutritional characteristics of these areas. Grazing intensity

was higher in areas with low forage quality when compared to other landscapes with higher quality forage. In particular, the Lower Kashunuk landscape experienced 27 and 40% higher grazing pressures than did Emperor Bend in 1994 and 1995, respectively, despite having both less available nitrogen (Table 6) and poor quality forage (Table 7). This pattern is curious since brant and other geese show some plasticity in brood site fidelity and dispersal to higher quality brood rearing areas would be likely to increase gosling fitness during this critical period of gosling growth (Hughes *et al.* 1994; Mark S. Lindberg, unpublished data). Our data are consistent with Cooch *et al.* (1993) who reported fidelity to deteriorating brood sites by snow geese when non-traditional sites of higher quality were available.

Geese are likely to respond to poor quality habitat in several ways; they may disperse to higher quality habitats, or they may compensate for poorer quality forage by increasing *per capita* intake. Apparent nitrogen offtake did not differ among brood-rearing areas within either colony, suggesting that geese may be able to compensate behaviorally for reduced biomass availability and poorer quality forage. Nonetheless, seasonal variation in gosling growth rates exist in this system suggesting goslings cannot fully compensate for variation in forage characteristics by increasing their intake (Sedinger and Flint 1991; Sedinger *et al.* 1997).

Conclusion

Population dynamics in breeding brant populations have been dramatically different at the Tutakoke River and Kokechik Bay colonies over past decades. We were

interested in the historical variation this comparison provided. Variation in grazing history between the Kokechik Bay and Tutakoke colonies over recent decades did not have a significant effect on the *NAPP* or forage quality of *C. subspathacea* lawns. This suggests that long term grazing by brant does not have deleterious effects in this ecosystem as has been documented in other goose grazing systems (Kerbes *et al.* 1990).

Most work on goose-grazing systems has addressed ecosystem structure and function, and has focused on cumulative seasonal plant growth in exclosures following grazing events. Some of this work has revealed that vegetation can overcompensate following herbivory, implying a positive feedback between some plants and their consumers. We investigated the response of vegetation to grazing pressure at a spatial and temporal scale relevant to the nutritional requirements of goslings. Despite observing dramatic differences in grazing intensities among landscapes, we found no effect of grazing on the *NAPP* of *C. subspathacea* during a period of the season when gosling growth is most sensitive to the quality and availability of forage. Finally, spatial variation in nitrogen concentration, availability of forage per sampled area, and quality of vegetation was greater than seasonal variation in these forage characteristics. This finding is profound given gosling growth and recruitment rates have been shown to be sensitive to relatively minor seasonal decreases in forage quality and availability, and it is likely that gosling growth rates vary spatially.

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Literature cited

Bazely, D. R. & Jefferies, R. L. (1985) Goose faeces: a source of nitrogen for plant growth in a grazed marsh. *Journal of Ecology*, **22**, 693-703.

Beaulieu, J., Gauthier G. & Rochefort, L. (1996) The growth response of graminoid plants to goose grazing in a high arctic environment. *Journal of Ecology*, **84**, 905-914.

Cargill, S. M. & Jefferies, R. L. (1984a) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 669 686.

Cargill, S. M. & Jefferies, R. L. (1984b) Nutrient limitation of primary production in a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 657-668.

Cooch, E. G., Lank, D. B., Duzbin, A., Rockwell, R. F., & Cooke F. (1991) Body size variation in Lesser Snow Geese: seasonal variation in gosling growth rate. *Ecology*, **72**, 503-512.

Cooch, E. G., Jefferies, R. L., Rockwell, R. F., & Cooke F. (1993) Environmental change and the cost of phylopatry: an example in the lesser snow geese. *Oecologia*, **93**, 128-138.

Derksen, D. V., Eldridge, W. D. & Weller, M. W. (1982) Habitat ecology of pacific black brant and other geese molting near Teshekpuk Lake, Alaska. *Wildfowl*, **33**, 39-57.

Eichholz, M. W. (1996) Body size, individual quality, and regulation of incubation in black brant. Masters thesis, University of Alaska, Fairbanks, Alaska.

Gadallah, F. L. & Jefferies, R. L. (1995) Comparison of the nutrient contents of the principal forage plants utilized by lesser snow geese on summer breeding grounds.*Journal of Applied Ecology*, **32**, 263- 275.

Gauthier, G., Hughes, R. J., Reed, A., Beaulieu, J. & Rochefort, L. (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653-664.

Goering, H. K. & Van Soest, P. J. (1970) Forage fiber analysis. U.S.D.A. *Agricultural Handbook*, **379**, 20 pp.

Hik, D. S. & Jefferies, R. L. (1990) Increases in the net above-ground primary production of a salt marsh forage grass: a test of the predictions of the herbivore optimization model. *Journal of Ecology*, **78**, 180-195.

Hik, D. S., Sadual, H. A. & Jefferies, R. L. (1991) Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. *Journal of Ecology*, **79**, 715-730.

Hughes, J. R., Reed, A. & Gauthier, G. (1994) Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. *Journal of Wildlife Management*, **58**, 536-545.

Kerbes, R. H., Kotanen, P. M., & Jefferies, R. L. (1990) Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology*, **27**, 242-258.

Klein, D. R. (1966) Waterfowl in the economy of the Eskimos on the Yukon Kuskokwim Delta, Alaska. *Journal of the Arctic Institute of North America*, **19**, 319-336.

Kincheloe, K. L. & Stehn, R. L. (1991) Vegetation patterns and environmental gradients in coastal meadows on the Yukon-Kuskokwim delta, Alaska. *Canadian Journal of Botany*, **69**, 1616-1627.

Kotanen, P. & Jefferies, R. L. (1987) The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. *Journal of Ecology*, **75**, 961-975.

Lang, K. K. & Raveling, D. G. (1993) Habitat and food selection by emperor goose goslings. *Condor*, **95**, 879-888.

Lindholm, A., Gauthier, G., & Desrochers, A. (1994) Effects of hatch date and food supply on gosling growth in arctic-nesting Greater Snow Geese. *Condor*, **96**, 898-908.

McNaughton, S. J. (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist*, **113**, 691-703.

McNaughton, S. J., Milchunas, D. G. & Frank, D. A. (1996) How can net primary productivity be measured in grazing ecosystems? *Ecology*, **77**, 974-977.

Maschinski, J. & Whitham, T. G. (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist*, **134**, 1-19.

Mitchell, S. F. & Wass, R. T. (1996) Quantifying herbivory: grazing consumption and interaction strength. *Oikos*, **76**, 573-576.

Mulder, C. P., Ruess, R. W. & Sedinger, J. S. (1996) Effects of environmental manipulations on *Triglochin palustris*: implications for the role of goose herbivory in controlling its distribution. *Journal of Ecology*, **84**, 267-278.

Ruess, R. W., Hik D. H. & Jefferies, R. L. (1989) The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. *Oecologia*, **79**, 23-29.

Ruess, R. W., Uliassi, D. D., Mulder, C. P. H. & Person, B. T. (1997) Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: Implications for geese-ecosystem dynamics in western Alaska. *EcoScience*, **4**, 170-178.

SAS Institute Inc. (1990) SAS/STAT *User's Guide*, Release 6.04 edition. SAS Institute Inc., Cary, North Carolina.

Sedinger, J. S. & Raveling, D. G. (1988) Foraging behavior of cackling Canada goose goslings: implications for the roles of food availability and processing rate. *Oecologia*, **75**, 119-124.

Sedinger, J. S. & Flint, P. L. (1991) Growth rate is negatively correlated with hatch date in black brant. *Ecology*, **72**, 496-502.

Sedinger, J. S., Lensink, C. J., Ward, D. H., Anthony, R. M., Wege, M. L. & Byrd, G. V. (1993) Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. *Wildfowl*, **44**, 49-59.

Sedinger, J. S., Flint, P. L. & Lindberg, M. S. (1995a) Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). *Ecology*, **76**, 2404-2414.

Sedinger, J. S., Eichholz, M. W. & Flint, P. L. (1995b) Variation in brood behavior of black brant. *Condor*, **97**, 107-115.

Sedinger, J. S., Lindberg, M.S., Eichholz, M. W. & Chelgren, N. (1997) Influence of hatch date versus maternal and genetic effects on growth of black brant goslings. *Auk*, **114**, 129-132

Srivastava, D. S. & Jefferies, R. L. (1995) The effect of salinity on the leaf and shoot demography of two arctic forage species. *Journal of Ecology*, **83**, 421-430.

Zellmer, I. D., Clauss, M. J., Hik, D. S. & Jefferies, R. L. (1993) Growth responses of arctic graminoids following grazing by captive lesser snow geese. *Oecologia*, **93**, 487-492

Table 2.1 Sampling schedule (Day/Month) for the growing seasons of 1994 and 1995. Treatment codes, with approximate sample interval, are as follows: (T0) initial sample, (O) grazed for 21 days, (X) exclosed for 21days, (OO) grazed for 42 days, (OX) grazed for 21 days and subsequently exclosed for 21 days, (XO) exclosed initially for 21 days and subsequently grazed for 21 days, (XX) exclosed for 42 days, (OOO) grazed for 54 days, and (OOX) grazed for 42 days and subsequently exclosed for 14 days.

COLONY	KASHUNUK DRAINAGE								KOKECHIK BAY			
LANDSCAPE	TUTAKOKE		LOWER KASHUNUK		ONUMTUK BEND		EMPEROR BEND		KOKECHIK WEST		KOLOMAK RIVER	
YEAR	1994	1995	1994	1995	1994	1995	1994	1995	-----	1995	-----	1995
TREATMENT												
T0	13/6	7/6	13/6	7/6	13/6	7/6	12/6	7/6	-----	10/6	-----	10/6
O , X	6/7	28/6	5/7	28/6	30/6	28/6	30/6	28/6	-----	30/6	-----	30/6
OO , OX , XO , XX	24/7	19/7	24/7	19/7	21/7	19/7	21/7	19/7	-----	20/7	-----	20/7
OOO , OOX	-----	2/8	-----	2/8	-----	2/8	-----	2/8	-----	2/8	-----	2/8

Table 2.2 Mean net above-ground primary productivity (*NAPP*) of the *Carex subspathacea* community across brood rearing areas used by geese nesting in the Tutakoke River black brant colony (Kashunuk drainage) on the Yukon-Kuskokwim Delta, Alaska during the 1994 and 1995 growing seasons and the Kokechik Bay black brant colony in 1995. Results are from ANOVA, Tukey's HSD method. Letters shared within columns are not statistically different at alpha = 0.05. Values represent mean ± SE g dwt m^{-2} d^{-1} from a sample size of 10 unless otherwise noted.

	NAPP FOR PERIOD 1				*NAPP* FOR PERIOD 2				*NAPP* FOR PERIOD 3	
KASHUNUK DRAINAGE	1994		1995		1994		1995		1995	
TUTAKOKE RIVER	A	1.32 ± 0.23	BC	1.42 ± 0.32	A	0.97 ± 0.20	AB	1.39 ± 0.17	AB	-0.02 ± 0.22
LOWER KASHUNUK	A	1.58 ± 0.25	A	2.28 ± 0.26	A	0.73 ± 0.62	B	2.16 ± 0.31	AB	0.11 ± 0.35
ONUMTUK BEND	A	0.77 ± 0.33	AB	1.86 ± 0.22	A	1.14 ± 0.23	A	1.08 ± 0.40	B	-0.30 ± 0.29
EMPEROR BEND	A	1.08 ± 0.37	A	2.42 ± 0.21	A	1.73 ± 0.21	A	0.79 ± 0.38	A	1.00 ± 0.50
KOKECHIK BAY										
KOKECHIK WEST		----	A	2.06 ± 0.45		----	A	1.32 ± 0.25[a]	A	1.13 ± 0.33
KOLOMAK RIVER		----	A	1.46 ± 0.43		----	A	1.59 ± 0.30	A	0.78 ± 0.32

[a] sample size = 8

TABLE 2.3 Landscape and treatment differences in standing crop biomass (g dwt m^{-2}) of *Carex subspathacea* swards on the Y-K Delta, AK in 1994 and 1995 growing seasons. Treatment codes are as follows: (T0) initial sample, (O) grazed for ≈ 21 days, (X) exclosed for ≈ 21d, (OO) grazed for ≈ 42 days, (OX) grazed for ≈ 21 days and subsequently exclosed for ≈ 21 days, (XO) exclosed initially for ≈ 21 days and subsequently grazed for ≈ 21 days, (XX) exclosed for ≈ 42 days, (OOO) grazed for ≈ 54 days, and (OOX) grazed for ≈ 42 days and subsequently exclosed for ≈ 14 days. Values presented are the mean ± SE based on a sample size of 10 unless otherwise noted. Letters shared within columns represent within-year and within-colony multiple comparisons (Tukey's HSD) of control plots and are not significantly different at alpha = 0.05. All overall ANOVA treatment effects used for linear contrasts between treatments had P values < 0.0001. Asterisks represent: (*) $P < 0.05$; (**) $P < 0.01$: (***) $P < 0.001$. Vegetation within the Kashunuk drainage differed in growth response following manipulation of grazing pressures in 1995 (landscape x treatment $F_{24,36} = 3.125$, $P < 0.0001$).

TREATMENT		T0	O	X	OO	OX	XO	XX	OOO	OOX
KASHUNUK DRAINAGE										
1994 Overall Linear Contrast			O vs X ***		OO vs OX ns : OO vs XO ns : XO vs XX ***					
1995 Overall Linear Contrast			O vs X ***		OO vs OX *** : OO vs XO ns : XO vs XX ***				OOO vs OOX ***	
LANDSCAPE / YEAR										
TUTAKOKE RIVER	1994	$A_{17.8 \pm 2.48}$	$A_{13.9 \pm 1.52}$	47.1 ± 4.17	$A_{17.7 \pm 1.34}$	59.1 ±4.30	20.9 ± 1.56	66.1 ± 5.52		
	1995	$A_{21.1 \pm 2.57}$	$A_{29.8 \pm 2.85}$	51.0 ± 6.95	$A_{26.9 \pm 2.22}$	32.4 ± 3.95	30.8 ± 2.93	106.2 ± 16.9	$A_{21.9 \pm 1.93}$	26.6 ± 3.95
LOWER KASHUNUK	1994	$AB_{36.1 \pm 7.07}$	$B_{41.6 \pm 8.28}$	70.9 ± 5.48	$B_{75.3 \pm 23.0}$	55.5 ± 13.2	77.6 ± 14.4	104.2 ± 17.2		
	1995	$A_{16.5 \pm 1.48}$	$A_{38.1 \pm 4.28}$	64.4 ± 4.81	$BC_{41.7 \pm 3.13}$	83.4 ± 4.88	78.6 ± 24.8	100.9 ± 11.1	$AB_{26.1 \pm 3.14}$	43.2 ± 4.11
ONUMTUK BEND	1994	$A_{32.8 \pm 3.21}$	$AB_{29.7 \pm 4.22}$	46.7 ± 6.46	$AB_{35.6 \pm 3.85}$	53.8 ± 7.17	43.3 ± 7.94	70.8 ± 7.46		
	1995	$A_{13.0 \pm 1.89}$	$A_{28.5 \pm 2.56}$	52.3 ± 6.10	$AB_{28.5 \pm 4.12}$	51.2 ± 8.27	31.9 ± 5.88	78.4 ± 6.94	$A_{20.4 \pm 3.08}$	24.3 ± 4.07
EMPEROR BEND	1994	$B_{52.2 \pm 5.16}$	$C_{62.7 \pm 5.48}$	71.7 ± 5.21	$B_{80.6 \pm 7.81}$	99.0 ± 6.91	94.7 ± 7.45	120.0 ± 10.5		
	1995	$B_{35.4 \pm 4.32}$	$B_{55.8 \pm 4.38}$	86.4 ± 4.77	$C_{46.1 \pm 7.01}$	72.5 ± 6.99	60.3 ± 10.5	122.2 ± 9.6	$B_{36.0 \pm 4.33}$	60.1 ± 8.32
KOKECHIK BAY										
1995 Overall Linear Contrast			O vs X ***		OO vs OX *** : OO vs XO ns : XO vs XX ***				OOO vs OOX **	
LANDSCAPE										
KOKECHIK WEST	1995	$A_{21.1 \pm 2.11}$	$A_{37.1 \pm 5.63}$	62.4 ± 9.24	$A_{32.4 \pm 7.56}$	71.3 ± 9.94[b]	39.3 ± 4.79[a]	76.1 ± 10.8	$A_{26.4 \pm 1.61}$	45.7 ± 9.89
KOLOMAK RIVER	1995	$B_{33.9 \pm 3.23}$	$A_{27.1 \pm 2.98}$	63.2 ± 9.47	$A_{37.2 \pm 3.80}$	58.9 ± 5.12	35.6 ± 5.17	83.0 ± 8.19	$A_{23.9 \pm 1.15}$	45.7 ± 9.89

[a] n = 9

[b] n = 8

Table 2.4 Mean apparent offtake of grazed plots in the *Carex subspathacea* community across brood rearing areas used by geese nesting at the Tutakoke River black brant colony (Kashunuk drainage) on the Yukon-Kuskokwim Delta, Alaska during the 1994 and 1995 growing seasons and the Kokechik Bay black brant colony in 1995. Results are from ANOVA, Tukey's HSD method. Letters shared within columns are not statistically different at alpha = 0.05. Values represent mean ± SE g dwt m^{-2} from a sample size of 10 unless otherwise noted.

	APPARENT OFFTAKE FOR PERIOD 1		APPARENT OFFTAKE FOR PERIOD 2		APPARENT OFFTAKE FOR PERIOD 3	
KASHUNUK DRAINAGE	1994	1995	1994	1995	1995	
TUTAKOKE RIVER	A 33.1 ± 3.7	A 21.2 ± 7.5	A 14.8 ± 3.8	AB 32.1 ± 3.1	B	4.7 ± 3.5
LOWER KASHUNUK	A 29.3 ± 8.2	A 26.3 ± 5.3	A -19.8 ± 22.0	A 41.8 ± 5.0	AB	17.1 ± 4.5
ONUMTUK BEND	A 17.1 ± 6.7	A 23.8 ± 4.6	A 1.1 ± 0.2	B 22.7 ± 6.8	B	3.9 ± 3.0
EMPEROR BEND	A 9.1 ± 6.8	A 30.7 ± 3.2	A 18.4 ± 6.7	AB 26.4 ± 4.2	A	24.1 ± 5.7
KOKECHIK BAY						
KOKECHIK WEST	----	A 30.1 ± 10.6	----	A 29.8 ± 6.4[a]	A	19.3 ± 9.9
KOLOMAK RIVER	----	A 36.0 ± 8.5	----	A 21.8 ± 3.5	A	23.5 ± 4.5

[a] sample size = 8

TABLE 2.5 Landscape and treatment differences in nitrogen concentration (as % dry mass) of *Carex subspathacea* swards on the Y-K Delta, AK in 1994 and 1995 growing seasons. Treatment codes follow those used in table 3. Values presented are the mean ± SE based on a sample size of 10 unless otherwise noted. Letters shared within columns represent within-year and within-colony multiple comparisons (Tukey's HSD) of control plots and are not significantly different at alpha = 0.05. All overall one-way ANOVA's used for linear contrasts between treatments had P values < 0.0001. Asterisks represent: (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

TREATMENT		T0	O	X	OO	OX	XO	XX	OOO	OOX
KASHUNUK DRAINAGE										
1994 Overall Linear Contrast			O vs X ns		OO vs OX ns : OO vs XO ns : XO vs XX **					
1995 Overall Linear Contrast			O vs X ***		OO vs OX *** : OO vs XO * : XO vs XX ***				OOO vs OOX *	
LANDSCAPE / YEAR										
TUTAKOKE RIVER	1994	$A_{4.16 \pm 0.23}$	$AB_{3.52 \pm 0.16}$	3.38 ± 0.17	$A_{3.75 \pm 0.12}$	3.44 ± 0.17	3.45 ± 0.12	2.63 ± 0.20		
	1995	$A_{4.39 \pm 0.15}$	$A_{3.19 \pm 0.39}$	3.45 ± 0.18	$A_{3.45 \pm 0.13}$[a]	2.92 ± 0.10	3.43 ± 0.20	2.41 ± 0.15	$A_{3.66 \pm 0.13}$	3.54 ± 0.14
LOWER KASHUNUK	1994	$A_{3.58 \pm 0.23}$	$B_{2.68 \pm 0.20}$	2.37 ± 0.19	$B_{2.41 \pm 0.32}$	2.42 ± 0.25	2.08 ± 0.20	1.92 ± 0.16		
	1995	$A_{4.22 \pm 0.16}$	$B_{3.48 \pm 0.12}$	2.82 ± 0.12	$A_{2.94 \pm 0.17}$	2.44 ± 0.15	2.56 ± 0.14	2.15 ± 0.11	$A_{3.35 \pm 0.21}$	2.96 ± 0.19
ONUMTUK BEND	1994	$A_{3.74 \pm 0.12}$	$A_{3.81 \pm 0.13}$	3.67 ± 0.11	$A_{3.53 \pm 0.17}$	3.28 ± 0.14	3.43 ± 0.17	3.00 ± 0.10		
	1995	$A_{4.46 \pm 0.11}$	$A_{4.11 \pm 0.16}$	3.77 ± 0.18	$A_{3.65 \pm 0.20}$	3.09 ± 0.16	3.50 ± 0.23	2.80 ± 0.17	$A_{3.85 \pm 0.23}$	3.61 ± 0.23
EMPEROR BEND	1994	$A_{3.65 \pm 0.09}$	$A_{3.51 \pm 0.08}$	3.37 ± 0.10	$A_{3.23 \pm 0.11}$	3.12 ± 0.05	3.01 ± 0.14	2.94 ± 0.09		
	1995	$A_{4.73 \pm 0.10}$	$A_{4.14 \pm 0.11}$	3.87 ± 0.11	$A_{3.65 \pm 0.18}$	3.72 ± 0.10	3.45 ± 0.20	3.33 ± 0.09	$A_{4.07 \pm 0.18}$	3.87 ± 0.15
KOKECHIK BAY										
1995 Overall Linear Contrast			O vs X ns		OO vs OX ns : OO vs XO ns : XO vs XX ns				OOO vs OOX *	
LANDSCAPE										
KOKECHIK WEST	1995	$A_{4.69 \pm 0.13}$	$A_{4.17 \pm 0.17}$	4.02 ± 0.18	$A_{3.63 \pm 0.19}$	3.08 ± 0.14[b]	3.35 ± 0.09[a]	3.17 ± 0.18	$A_{3.67 \pm 0.07}$	2.99 ± 0.13
KOLOMAK RIVER	1995	$B_{3.85 \pm 0.13}$	$A_{3.65 \pm 0.12}$	3.19 ± 0.19	$A_{3.21 \pm 0.13}$	3.04 ± 0.16	3.04 ± 0.16	2.63 ± 0.25	$A_{3.67 \pm 0.07}$	3.37 ± 0.15

[a] $n = 9$

[b] $n = 8$

TABLE 2.6 Landscape and treatment differences in standing crop nitrogen (g N m^{-2}) of *Carex subspathacea* swards on the Y-K Delta, AK in 1994 and 1995 growing seasons. Treatment codes follow those used in table 3. Values presented are the mean ± SE based on a sample size of 10 unless otherwise noted. Letters shared within columns represent within-year and within-colony multiple comparisons (Tukey's HSD) of control plots and are not significantly different at alpha = 0.05. All overall one-way ANOVA's used for linear contrasts between treatments had P values < 0.0001. Asterisks represent: (*) P < 0.05; (**) P < 0.01: (***) P < 0.001. Standing crop nitrogen within the Kashunuk drainage differed following manipulation of grazing pressures in 1994 and 1995 (1994 landscape x treatment $F_{18,36} = 2.62$, $P < 0.01$; 1995 landscape x treatment $F_{24,36} = 4.013$, $P < 0.0001$).

TREATMENT		T0	O	X	OO	OX	XO	XX	OOO	OOX
KASHUNUK DRAINAGE										
1994 Overall Linear Contrast			O vs X ***		OO vs OX ** : OO vs XO ns : XO vs XX ***					
1995 Overall Linear Contrast			O vs X ***		OO vs OX *** : OO vs XO** : XO vs XX ***				OOO vs OOX ***	
LANDSCAPE / YEAR										
TUTAKOKE RIVER	1994	$A_{0.71 \pm 0.08}$	$C_{0.49 \pm 0.05}$	1.58 ± 0.16	$C_{0.65 \pm 0.04}$	1.07 ± 0.08	0.71 ± 0.05	1.70 ± 0.16		
	1995	$A_{0.92 \pm 0.11}$	$A_{0.89 \pm 0.13}$	1.68 ± 0.16	$B_{0.92 \pm 0.07}$[a]	1.71 ± 0.12	1.03 ± 0.08	2.40 ± 0.23	$A_{0.78 \pm 0.05}$	0.92 ± 0.13
LOWER KASHUNUK	1994	$A_{1.20 \pm 0.18}$	$B_{1.00 \pm 0.13}$	1.66 ± 0.17	$B_{1.30 \pm 0.21}$	1.10 ± 0.18	1.42 ± 0.15	1.89 ± 0.25		
	1995	$A_{0.70 \pm 0.07}$	$A_{1.33 \pm 0.17}$	1.83 ± 0.18	$AB_{1.19 \pm 0.07}$	2.00 ± 0.13	2.04 ± 0.71	2.14 ± 0.24	$A_{0.83 \pm 0.07}$	1.24 ± 0.10
ONUMTUK BEND	1994	$A_{1.22 \pm 0.11}$	$B_{1.09 \pm 0.12}$	1.71 ± 0.24	$B_{1.23 \pm 0.11}$	1.69 ± 0.19	1.42 ± 0.20	2.10 ± 0.19		
	1995	$A_{0.57 \pm 0.08}$	$A_{1.16 \pm 0.10}$	1.95 ± 0.22	$B_{0.99 \pm 0.13}$	1.51 ± 0.17	1.01 ± 0.14	2.16 ± 0.19	$A_{0.75 \pm 0.11}$	0.85 ± 0.14
EMPEROR BEND	1994	$B_{1.89 \pm 0.17}$	$A_{2.17 \pm 0.16}$	2.40 ± 0.17	$A_{2.56 \pm 0.18}$	3.07 ± 0.19	2.78 ± 0.12	3.54 ± 0.34		
	1995	$B_{1.64 \pm 0.17}$	$B_{2.27 \pm 0.13}$	3.31 ± 0.14	$A_{1.62 \pm 0.21}$	2.66 ± 0.21	1.96 ± 0.28	4.02 ± 0.26	$B_{1.40 \pm 0.12}$	2.23 ± 0.26
KOKECHIK BAY										
1995 Overall Linear Contrast			O vs X ***		OO vs OX *** : OO vs XO ns : XO vs XX ***				OOO vs OOX **	
LANDSCAPE										
KOKECHIK WEST	1995	$A_{1.30 \pm 0.12}$	$A_{0.98 \pm 0.11}$	1.91 ± 0.22	$A_{1.15 \pm 0.09}$	1.74 ± 0.14[b]	1.04 ± 0.12[a]	2.04 ± 0.15	$A_{0.88 \pm 0.05}$	1.62 ± 0.20
KOLOMAK RIVER	1995	$B_{0.98 \pm 0.09}$	$B_{1.51 \pm 0.22}$	2.39 ± 0.32	$A_{1.09 \pm 0.17}$	2.13 ± 0.25	1.31 ± 0.14	2.31 ± 0.28	$A_{0.97 \pm 0.05}$	1.40 ± 0.33

[a] $n = 9$

[b] $n = 8$

TABLE 2.7 Landscape and treatment differences in the carbon to nitrogen ratio (C:N) of *Carex subspathacea* swards on the Y-K Delta, AK in 1994 and 1995 growing seasons. Treatment codes follow those used in table 3. Values presented are the mean ± SE based on a sample size of 10 unless otherwise noted. Letters shared within columns represent within-year and within-colony multiple comparisons (Tukey's HSD) of control plots and are not significantly different at alpha = 0.05. All overall one-way ANOVA's used for linear contrasts between treatments had P values < 0.0001. Asterisks represent: (*) P < 0.05; (**) P < 0.01: (***) P < 0.001. The C:N ratio of swards within the Kashunuk drainage differed following manipulation of grazing pressures in 1995 (1995 landscape x treatment $F_{24,36} = 2.42$, $P < 0.01$).

TREATMENT		T0	O	X	OO	OX	XO	XX	OOO	OOX
KASHUNUK DRAINAGE										
1994 Overall Linear Contrast			O vs X ns		OO vs OX ns : OO vs XO ns : XO vs XX **					
1995 Overall Linear Contrast			O vs X ***		OO vs OX *** : OO vs XO ns : XO vs XX ***				OOO vs OOX ns	
LANDSCAPE / YEAR										
TUTAKOKE RIVER	1994	$AB_{10.2 \pm 0.5}$	$B_{10.7 \pm 0.4}$	12.6 ± 0.6	$B_{11.1 \pm 0.4}$	12.3 ± 0.3	12.4 ± 0.4	15.4 ± 0.7		
	1995	$AB_{9.9 \pm 0.3}$	$A_{11.3 \pm 1.4}$	13.1 ± 0.7	$AB_{12.6 \pm 0.6}$[a]	15.1 ± 0.6	12.6 ± 0.7	17.5 ± 1.1	$A_{12.3 \pm 0.5}$	12.9 ± 0.5
LOWER KASHUNUK	1994	$A_{12.0 \pm 0.9}$	$A_{15.5 \pm 1.6}$	18.6 ± 1.6	$A_{20.1 \pm 3.2}$	19.1 ± 2.6	21.2 ± 2.3	22.0 ± 2.1		
	1995	$A_{10.0 \pm 0.1}$	$A_{12.8 \pm 0.5}$	15.7 ± 0.6	$B_{14.5 \pm 1.1}$	18.2 ± 1.3	16.4 ± 1.2	20.2 ± 0.9	$A_{13.2 \pm 0.8}$	15.1 ± 1.0
ONUMTUK BEND	1994	$AB_{9.7 \pm 0.4}$	$B_{10.5 \pm 0.3}$	11.4 ± 0.3	$B_{11.4 \pm 0.5}$	12.6 ± 0.4	11.8 ± 0.5	13.6 ± 0.4		
	1995	$AB_{9.6 \pm 0.2}$	$B_{10.4 \pm 0.4}$	11.6 ± 0.6	$AB_{11.4 \pm 0.6}$	13.9 ± 0.7	12.2 ± 0.8	15.5 ± 1.0	$A_{12.0 \pm 0.8}$	12.6 ± 0.7
EMPEROR BEND	1994	$B_{10.4 \pm 0.2}$	$B_{11.7 \pm 0.3}$	12.2 ± 0.3	$AB_{13.1 \pm 0.4}$	13.4 ± 0.2	13.9 ± 0.6	14.4 ± 0.5		
	1995	$B_{9.1 \pm 0.2}$	$B_{10.1 \pm 0.2}$	11.4 ± 0.3	$A_{10.5 \pm 0.3}$	11.0 ± 0.2	11.2 ± 0.4	12.6 ± 0.3	$A_{10.8 \pm 0.5}$	11.4 ± 0.3
KOKECHIK BAY										
1995 Overall Linear Contrast			O vs X ns		OO vs OX ns : OO vs XO ns : XO vs XX **				OOO vs OOX *	
LANDSCAPE										
KOKECHIK WEST	1995	$A_{11.4 \pm 0.4}$	$A_{11.9 \pm 0.4}$	13.4 ± 0.6	$A_{13.5 \pm 0.5}$	14.2 ± 0.6[b]	14.2 ± 0.7[a]	17.1 ± 1.0	$A_{12.2 \pm 0.3}$	13.2 ± 0.7
KOLOMAK RIVER	1995	$B_{9.5 \pm 0.2}$	$B_{10.5 \pm 0.4}$	11.2 ± 0.5	$B_{11.5 \pm 0.7}$	13.6 ± 0.6	12.1 ± 0.4	13.3 ± 0.7	$A_{12.2 \pm 0.3}$	14.7 ± 0.6

[a] $n = 9$

[b] $n = 8$

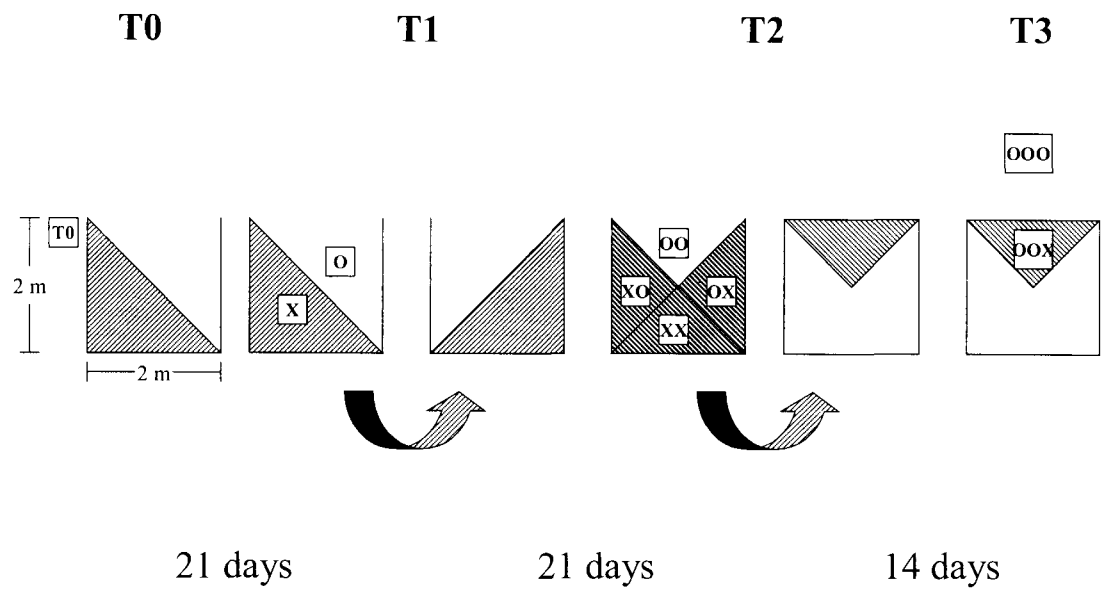

Figure 2.1. Design of three-sided exclosures. T0 = initial harvest; T1 (21 days) = harvest of 1 grazed turf (O), and 1exclosed turf (X); T2 (42 days) = harvest of 1 turf grazed for 42 days (OO), 1 turf exclosed for 42 days (XX), 1 turf grazed for 21 days and subsequently exclosed (OX), 1 turf exclosed for 21 days and subsequently grazed (XO); T3 (56 days; 1995 only) = harvest of 1 turf grazed for 56 days (OOO), 1 turf grazed for 42 days and subsequently exclosed for 14 days (OOX). At T1 and T2 (1995 only) exclosed positions were switched.

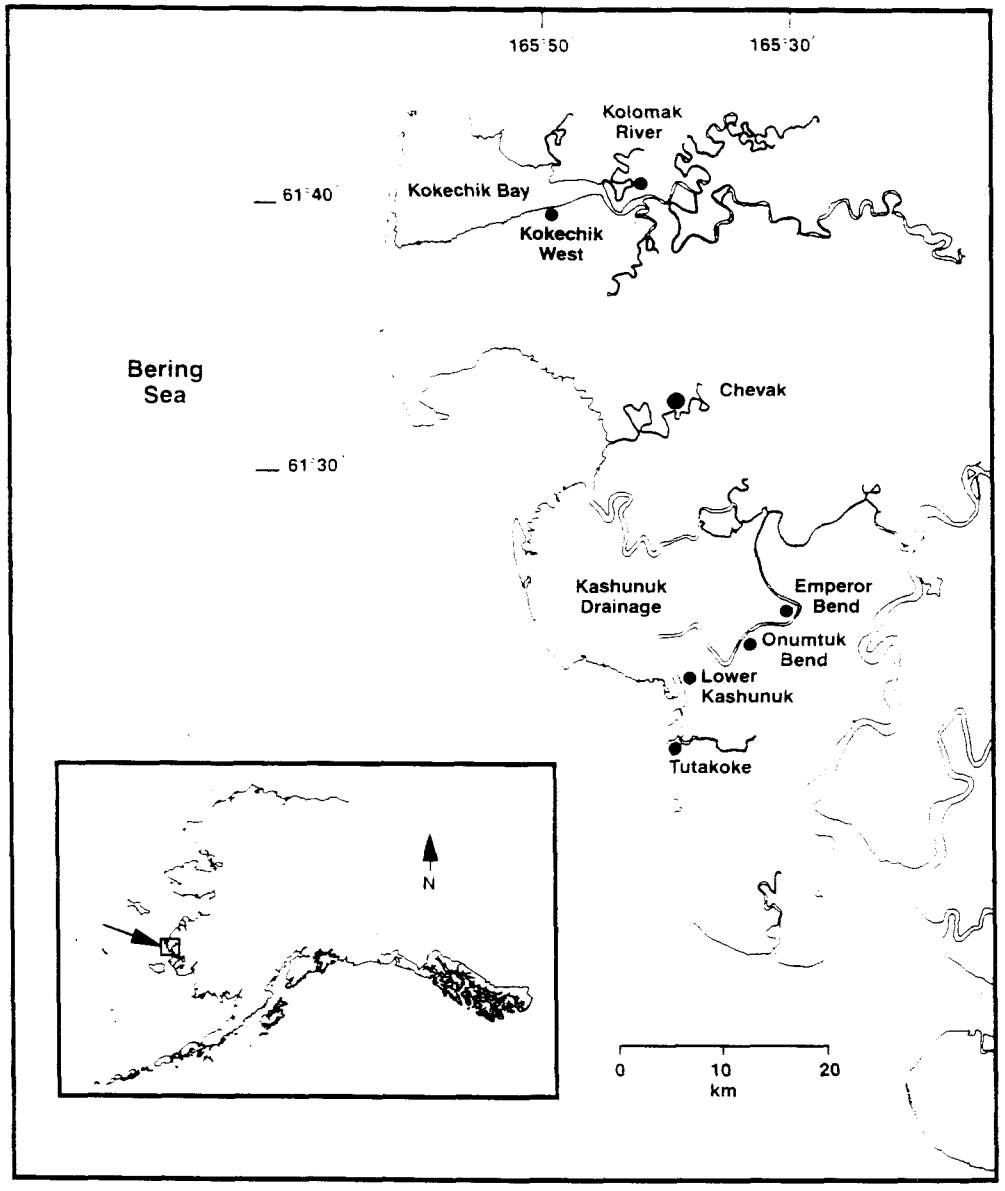

Figure 2.2. Study area on the Yukon-Kuskokwim Delta, Alaska. Black brant colonies are centred on the Tutakoke and Kokechik West site.

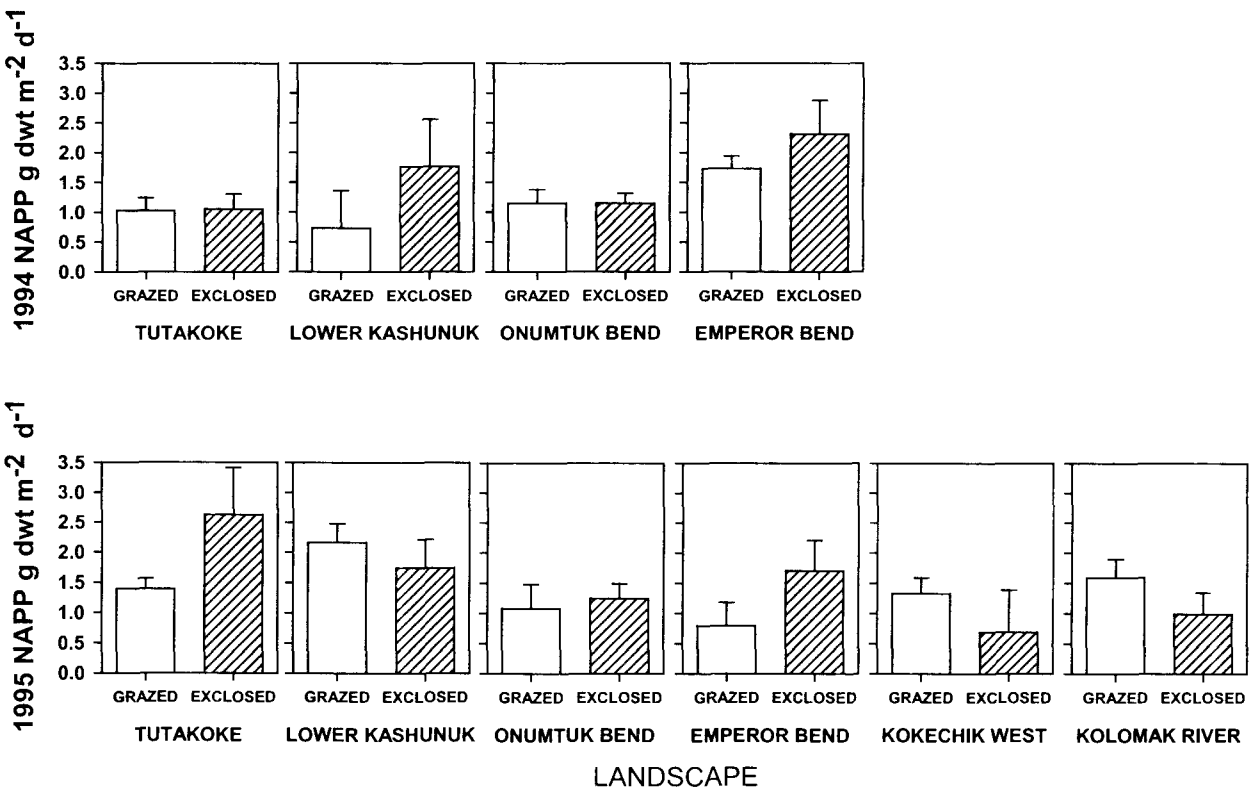

Figure 2.3. Comparison between net above-ground primary productivity (*NAPP*) of *Carex subspathacea* swards grazed early in the growing season and *NAPP* of *C. subspathacea* swards exclosed throughout the early- and mid-season. All linear contrasts had *P* values > 0.05.

CHAPTER 3. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth[3]

Abstract This study focuses on the effects of grazing by Black Brant geese (hereafter Brant) on plant community zonation and the associated effects on gosling growth between 1987 – 2000 at a nesting colony in southwestern Alaska. We observed that when heavily grazed, *Carex ramenskii* attains a short character state that serves as a nutritional surrogate for the preferred forage of Brant, *C. subspathacea* grazing lawns. This work couples a manipulative experiment designed to initiate the creation of grazing lawns with long-term mark-recapture work and estimates of the areal extent of the dominant plant communities used by breeding Brant.

We mowed plots of ungrazed *C. ramenskii* meadows to create swards that Brant then selected and maintained as grazing lawns. Faecal counts, an index of grazing intensity, averaged 26 m^{-2} on mowed plots and 3 m^{-2} on control plots, indicating Brant selected manipulated swards in the year following treatment application. Both nutritional quality and aboveground biomass of mowed plots were similar to that of *C. subspathacea* grazing lawns. We marked and recaptured 1,302 known-age goslings between 1987 – 1998. Goslings were largest between 1987 – 1989 when the Tutakoke population was first beginning to recover from harvest and predation pressures. Gosling mass then decreased between 1989 – 1992 due to density dependent effects. Between 1993 and

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1998 gosling mass increased despite a local population trajectory characteristic of a population that has reached carrying capacity. The number of families reared from the Tutakoke colony increased from 885 to 4,165 pairs between 1987 – 1991 after which time the population remained roughly stable, yet below historical densities. In the Tutakoke River colony, grazing lawns increased from 3 to 8 % coincident with a decrease in the areal extent of *C. ramenskii* meadows, suggesting that there was a large-scale conversion between these two communities between 1991 and 1999.

Removing aboveground tissues of *C. ramenskii* resulted in a sward that Brant select and can maintain in a character state that serves as a nutritional surrogate to their preferred forage. We suggest that the areal extent of grazing lawns is dependent on the population size of herbivores. Under high-density conditions, Brant trigger a vegetation conversion that favors the growth of young. Because larger goslings have increased survival, breeding probability, and fecundity, we predict that these herbivore-mediated changes in the distribution of plant communities will result in a positive numerical response of the population within the next two decades.

Key words: plant-animal interactions; phenotypic plasticity; geese; *Carex spp.*; salt marsh.

Introduction

Density dependent conditions force herbivores either to switch to alternative foods or to move to areas that have greater available resources (Vickery et al. 1995). Breeding geese switch to alternative foods that are lower in quality when preferred

resources are depleted because they demonstrate both fidelity to their breeding grounds and a faithfulness to brood rearing areas (Cooch et al. 1993; Hughes et al. 1994; Gadallah and Jefferies 1995; Lindberg et al. 1998). However, herbivory modifies the habitat in ways that can have either positive or negative effects on its capacity to support secondary production (Kerbes et al. 1990; McNaughton et al. 1997). A population of Black Brant geese (*Branta bernicla nigricans*, hereafter Brant) nesting at the Tutakoke River colony on the Yukon-Kuskowim Delta (YK) in southwestern Alaska appears to be at carrying capacity below historic densities (Sedinger et al. 1998). Adult Brant grazing pressure on *Carex ramenskii* has increased over the past decade despite its lower nutritive quality than that of *C. subspathacea* grazing lawns, Brant's preferred forage (Ruess et al. 1997; Person et al. 1998; BT Person *unpub. data*). *C. ramenskii* and *C. subspathacea* were classified as conspecifics (*See Study Area, Taxonomic issues and plant communities in the Tutakoke River colony*) until they were separated in the late 1930's based largely on tiller length and floral position (Hultén 1941; Hultén 1990). We present both experimental and long-term data that as we interpret it, suggests grazing by Brant is reverting *C. ramenskii* meadows into grazing lawns that are indiscernible from those of *C. subspathacea*. Because the nutritional environment in which a gosling is reared is the principle determinant of their size at fledging (Cooch et al. 1991; Larsson and Forslund 1991; Sedinger et al. 1995; Sedinger et al. 1998) we relate an anomalous increase in gosling mass, observed under density dependent conditions, to changes in the extent of grazing lawns within the Tutakoke River colony.

Herbivores influence, and in some cases can regulate, forage quality and availability through changes in plant growth, community composition, and rates and pathways of nutrient cycling (Coppock et al. 1983a; Bazely 1986; Ruess et al. 1989; Hik and Jefferies 1990; Pastor and Naiman 1992; Mulder and Ruess 1998). These effects can have positive or negative feedbacks to herbivores depending on the spatial and temporal magnitude of tissue removal and successional state of the ecosystem (Kerbes et al. 1990; Pastor et al. 1997). In terrestrial grazing systems, feedbacks to herbivore nutrition, growth, and life history have more or less been inferred from modeling approaches, animal condition and fecundity, and changes in the availability and quality of forage (Hobbs and Swift 1985; Coughenour and Singer 1996; Pastor and Cohen 1997; Singer et al. 1997). Perhaps the most detailed understanding of these feedbacks comes from studies of geese, where gosling growth has been shown to be highly sensitive to the quality and *per capita* availability of foods, and where population dynamics can be followed using marked individuals (Cooch et al. 1991; Larsson and Forslund 1991; Sedinger and Flint 1991; Lindholm et al. 1994). For example, size of goslings at fledging influences first year survival, adult body size, and adult fitness (Cooch et al. 1993; Larsson and Forslund 1991; Sedinger et al. 1995). It follows that vegetation quality and availability may have impacts on the demography and size of herbivore populations (Oesterheld et al. 1992; Cooch et al. 1993).

Like other terrestrial herbivores (McNaughton 1984; Coppock et al. 1983b), geese often create and maintain grazing lawns, defined here as vegetation swards dominated by a high density of grazing-tolerant plant species with high nutrient concentrations.

Maintenance of these swards by herbivores results in a high biovolume of nutritious forage. Grazing lawns range from a few square meters (Person et al. 1998) to square kilometers (McNaughton 1983; 1985), influenced principally by herbivore densities and landscape structure. The structural and functional stability of grazing lawns is sensitive to the activities of herbivores (Bazely and Jefferies 1985; McNaughton 1997), abiotic factors such as soil salinity and precipitation (East 1984; Srivastava and Jefferies 1995), and human impacts (Oesterheld et al. 1992; Jefferies et al. 1994). Despite the close association between herbivores and their food resources in systems where grazing lawns are a prominent feature of the ecosystem, no study has demonstrated the creation of these lawns and coupled it with effects on wild herbivore growth at the population-level.

Here we show that after aboveground *C. ramenskii* tissues are experimentally removed, Brant select the remaining tissues as a food source. We demonstrate that for five years Brant have maintained some of these grazing lawns that function as a nutritional surrogate to their preferred food, *C. subspathacea*. We then present evidence that the areal extent of *C. ramenskii*-dominated meadows has decreased throughout the Tutakoke River colony landscape over the past decade concurrent with an increase in the extent of grazing lawns. We then show that gosling mass increased between 1992 – 1998 despite observations that the population appears to be at a carrying capacity below historic densities. We conclude by suggesting that (i) the areal extent of grazing lawns is dependent on population size, and that (ii) density dependent effects on animal growth can be modified by herbivores; and finally, we offer (iii) a hypothesis that these

herbivore-mediated changes could translate into a numerical increase in this population over the next two decades.

Methods

Study system

Population dynamics, and nutritional considerations

This study was conducted at the Tutakoke River Brant colony (61° 15' N, 165°30' W) at the mouth of the Kashunuk River and Angyoyaravak Bay, where research begun in 1985 has resulted in the marking of approximately 30 % of the individuals breeding at the colony. Historically, Brant nested in a band that stretched from the present colony to approximately 20 km up the Kashunuk River drainage (Spencer et al. 1951; King and Derksen 1986). This distribution was reduced from 7400 to 1100 nesting pairs during the late 1970's and early 1980's coincident with heavy arctic fox predation and the advent of outboard motors into the subsistence culture of the people of this region (Raveling 1986; Anthony et al. 1991; Sedinger et al. 1993; Anthony et al. 1995; Sedinger 1996). Reduced harvest and predation has allowed the population to increase to 5500 pairs where it has stabilized below historic densities (Raveling 1989; Sedinger et al. 1993; Anthony et al. 1995). Density dependent reductions in growth, body size, and clutch size in Brant nesting at Tutakoke initially accompanied the population increase (Sedinger et al. 1998). Sedinger et al. (1998) argued that these effects were independent of harvest and predation pressures and were associated with changes in the forage base on the breeding grounds.

Brant goslings are sensitive to foods high in fibre relative to their protein content owing to their simple digestive system, small body size, and high metabolic demands associated with growth (Demment and VanSoest 1985; Sedinger and Raveling 1984; Sedinger and Raveling 1988). Growth rates of goslings are among the highest of precocial birds and are limited by the nitrogen content of foods such that goslings reared on lower quality foods are smaller (Lieff 1973; Rickleffs 1973; Sedinger and Flint 1991; Sedinger 1997). Smaller goslings have lower first year survival, recruitment rates, and produce fewer offspring if they are recruited into the population (Cooch et al. 1993; Larsson and Forslund 1991; Sedinger et al. 1995). However, adult Brant are capable of replenishing nutrient reserves lost during breeding and moulting while feeding on foods of lower quality than those used by goslings in part because of the positive relationships between body and gut size, and between protein and energy use efficiencies (Demment and VanSoest 1985; Buchsbaum et al. 1986; Sedinger 1997).

Taxonomic issues and plant communities in the Tutakoke River colony

The YK Delta is one of the largest expanses of salt marsh in North America, encompassing over 75,000 km^2 of wetlands between the Yukon and Kuskokwim Rivers. The coastal zone of this region supports some of the largest, and perhaps most diverse, breeding assemblages of waterfowl and shorebirds in the circumpolar subarctic (Bellrose 1980, Gill and Handel 1990). Throughout the coastal fringe of the YK Delta, *C. subspathacea*, the preferred forage of Brant, occurs as nearly monospecific grazing lawns that are maintained by grazing whereas *C. ramenskii* occurs as a taller sedge whose nutritional quality is lower than that of *C. subspathacea* (Sedinger et al. 1995; Ruess et al.

1997; Person et al. 1998). These two sedges were classified as conspecifics until the late 1930's at which time they were re-classified as separate species based largely on their tiller length and floral position (Hultén 1941). While the demarcation of these two sedges may have been warranted, they remain to be differentiated at the genetic level. We follow the present classification scheme (Hultén 1990) but believe a genetic description is needed because the data presented herein provides ecological evidence that these sedges may be conspecifics whose morphology is controlled by grazing pressure.

Three plant communities dominate areas used by Brant at the Tutakoke River colony: a slough levee community, *C. subspathacea* grazing lawns, and *C. ramenskii*-dominated meadows. The slough levee community occurs on elevated beach ridges and depositional levees along drainages that dissect the region. Geese forage selectively in this community for *Triglochin palustris* (Mulder et al. 1996; Mulder and Ruess 1998). *C. subspathacea* is maintained by Brant as short (0.5-3 cm height) grazing lawns occurring along coastal margins, riparian mudflats, and inland pond margins. Brant spend a disproportionate amount of time foraging on this community relative to its distribution and consume over 90% of the annual net aboveground primary productivity with no apparent negative effects on aboveground growth (Sedinger et al. 1995; Person et al. 1998). When protected from herbivores for 2 years, *C. subspathacea* can reach an aboveground biomass, nutritional quality, and growth form that does not differ from *C. ramenskii*, a taller (20-50 cm), less preferred forage of Brant (B.T. Person unpublished data). *C. ramenskii*-dominated meadows comprise the greatest areal extent of the 3

communities, and *C. ramenskii* itself constitutes 60-70% of the aboveground live biomass of this community.

Grazing pressure on *C. ramenskii* is both temporally and spatially patchy and tied to spring snowmelt patterns. For example, in 2001 we followed and sampled *C. ramenskii* meadows 3 weeks following spring snow melt in areas that were snow-free several weeks before the majority of *C. ramenskii* and *C. subspathacea* habitat became available. Standing crop biomass (SCB) of these grazed areas averaged 43 ± 6 g dwt m^{-2} compared to 76 ± 5 g dwt m^{-2} in ungrazed areas. The number of grazing scars, which averaged 97 and 23 % of the tillers in the two areas, distinguished grazed and ungrazed areas, respectively. Trampling by geese decreased the standing dead in areas that first became available during spring break-up. Standing dead biomass averaged 13 ± 4 g dwt m^{-2} and 237 ± 5 g dwt m^{-2} in grazed and ungrazed *C. ramenskii* meadows, respectively. Throughout the Kashunuk River drainage *C. ramenskii* occurs in patchy assemblages of these short, heavily grazed, and tall, ungrazed, character states, *i.e.*, distinct phenotypic states (*sensu* Stearns 1992), the short character state appearing identical to *C. subspathacea* grazing lawns. Since 1991 we have observed an increase in these assemblages throughout the Kashunuk River drainage.

Mowing experiment

In 1995, we initiated an experiment in which we mowed and removed cuttings from plots within *C. ramenskii* meadows in three locations across the Tutakoke River colony. We attempted to create swards that Brant would select and subsequently maintain as grazing lawns. We established 4 15 x 15 m treatment plots at 2 of our 3

replicates (see below). Landscape structure differed at the third location such that plant community zonation occurred over a few meters in contrast to the other 2 locations where community zonation occurred over hundreds of meters. Because the landscape was more finely dissected at this location, we established plots that totaled 225 m^2. At all locations we established unfenced:

(1) control plot within meadows of ungrazed *C. ramenskii*.

(2) areas we called "dynamic control plots", or grazed hot spots where geese were feeding on *C. ramenskii* and creating a patchy assemblage of short- and tall-form *C. ramenskii*, as described above.

(3) a mowed plot adjacent to the dynamic control plot where we clipped *C. ramenskii* meadows to a canopy height of 5 cm and removed cuttings (termed "adjacent-clipped", hereafter AC treatment plots).

(4) another mowed plot identical to (3) but approximately 150 m distant in an ungrazed *C. ramenskii* meadow (termed "distant clipped", hereafter DC treatment plots). We included the DC treatment plots because geese may have chosen and maintained the AC plots simply because these plots were adjacent to areas already grazed, as opposed to selecting an artificially-created forage patch in the middle of a previously ungrazed meadow. Treatments were applied in early-June and mid-July of 1995 only.

Aboveground biomass was sampled by clipping vegetation to the soil surface within 5 10 x 10 cm quadrats. Vegetation samples were washed in fresh water, sorted to species (Hultén 1990) and standing dead, dried in a field laboratory at 60° C, and stored for shipment to the University of Alaska Fairbanks where they were dried to constant

mass at 60° C and weighed to the nearest 0.01 g. We estimated net aboveground primary productivity (*NAPP*) using movable exclosure techniques in 1996 and 1997. Briefly, we randomly placed 5 30 cm diameter exclosures within all treatment plots 2 and 3 times in 1996 and 1997, respectively. We estimated *NAPP* as the difference between biomass within short-term exclosures and unexclosed biomass sampled at the time exclosures were established, divided by interval days. We sampled aboveground biomass from 5 independent, unexclosed and exclosed turves each time *NAPP* estimates were made in order to avoid potential autocorrelational problems (Mitchel and Wass 1996). Vegetation within exclosures was sampled and processed as previously described. In 2000, we re-visited all plots but only sampled SCB and grazing intensity from plots at one of the three locations because vegetation at the other locations was not visibly different from *C. ramenskii* meadows surrounding the manipulated plots.

We measured nitrogen and carbon content of *C. ramenskii* by combusting vegetation in a LECO CNS 2000 autoanalyzer (Michigan, MI) after grinding vegetation through a 20-mesh size Wiley Mill. We report the carbon to nitrogen ratio (C:N) of *C. ramenskii* as an additional index of forage quality. Higher C:N ratios represent poorer quality forage because geese, particularly goslings, face gut volume constraints (Sedinger and Raveling 1988). Thus, C:N ratios are an index of the concentration of structural fibre relative to the nitrogen content of vegetation. We use faecal counts as an estimate of grazing intensity. Faecal counts were made within randomly thrown 1 m^2 quadrats each time vegetation was sampled. Statistical analyses were performed on faecal counts taken at the end of each growing season.

Our experiment was a randomized complete block design with location as the level of replication. Data were analyzed using ANOVA with year and location as class variables, 1996 and 1997 only. We included all two- and three-way interactions and removed them if they were not significant. We found a significant year * treatment * location interaction when either aboveground biomass or faecal counts were dependent variables. Therefore, these data were analyzed using one-way ANOVA followed by Tukey's honest significant difference (HSD) multiple comparisons when a significant treatment effect was found. Data were analyzed using General Linear Model (GLM) procedures (SAS Institute Inc., 1990). Data were rank transformed, where necessary, in order to meet model assumptions.

Changes in the zonation of plant communities

We estimated the areal extent of plant communities at the Tutakoke colony from aerial videography tapes filmed to estimate the number of Brant nesting at the approximate 10 km^2 Tutakoke colony (Anthony et al. 1995). Methods for filming aerial videography are reported in Anthony et al. (1995). Briefly, videography was recorded by attaching a Hi 8 colour video camera to a fixed wing aircraft. Between 1991 and 1999, 27 different random transects, each approximately 3 km long, were flown annually. Transects were not flown in 1996.

In all years for which transects were flown, vegetation type was identifiable on each video image except in 1992, which was not analyzed. We estimated the percent cover of physiographic features and plant communities throughout the Tutakoke colony by taping a clear plastic sheet printed with 100, 1.0 mm diameter circles to a viewing

monitor. We then identified plant communities within each circle as either *C. subspathacea* grazing lawn, *C. ramenskii*-dominated meadows, or slough levee communities. We also identified the areal extent of the following physiographic features: lakes, rivers and tidal sloughs, mudflats, and miscellaneous features (*e.g.*, driftwood, geese, nests, observation towers) which were classified as 'other'.

We hypothesized that there would be an increase in the areal extent of *C. subspathacea* grazing lawns concurrent with a decline in the extent of *C. ramenskii*-dominated meadows throughout the 1990's. To test this hypothesis, we first regressed the percent cover of each community type at Tutakoke against time, and tested for the departure of each slope from zero. We then tested for an inverse relationship between these models by comparing the absolute values of the slopes from the *C. subspathacea* and *C. ramenskii* regression models using a *Z*-test (Zar 1996). Data were arcsine transformed and analyzed using regression procedures (SAS Institute Inc. 1990).

Changes in gosling mass

Between 1985 and 1997 we searched 67 random 50 m diameter plots for Brant nests annually. We also attempted to find all nests associated with a male or female Brant marked with an individually coded alpha-numeric tarsal band both on and off plots. All nests and eggs within clutches were marked when found (Sedinger et al. 1995). At hatch we revisited all marked nests and attempted to mark all goslings with a uniquely numbered fish-fingerling tag stapled through the web of their foot as they were hatching. Approximately 32 d later, we conducted banding drives while geese were flightless. Geese were herded into temporary corrals on a sample of brood rearing areas used by

Brant families from the Tutakoke River colony. Sex was determined by cloacal examination on all goslings marked with a fingerling tag and gosling mass was measured (± 5.0 g) with a spring scale. Goslings were then marked with a uniquely coded alpha-numeric tarsal band and released after all birds had been processed for a particular banding drive. This methodology allows an estimate of gosling age ± 36 h because all goslings within a clutch hatch and depart their nest within a 36 h period (Sedinger et al. 1998).

We tested for variation in gosling mass using ANCOVA (SAS Institute Inc., 1990). We entered gosling sex and year as class variables, and gosling age as a covariate, and included age * year interactions.

Estimating the number of families reared from the Tutakoke river colony

We estimated the number of families reared from the Tutakoke river colony using a Lincoln-Peterson index (Poole 1974). We used the number of marked females observed during nesting as an initial sample of the number of nesting pairs using brood rearing areas that we sampled approximately 32 days later. We then used a ratio of the number of unmarked and marked females captured during banding drives to calculate an index of the number of families using brood rearing areas (Sedinger et al. 1998).

We include estimates of the number of Brant nesting at the Tutakoke River colony between 1991 – 2000 (Anthony 2001). Methods for estimating the nesting population are presented in Anthony et al. (1995) and represent the number of Brant nesting in mid-June, approximately midway through incubation. We include estimates of nesting Brant because our brood estimates are a conservative estimate of the breeding

population at Tutakoke. Brood estimates do not include those birds whose nests were destroyed by either predators or abiotic events such as storm surges.

Results

Mowing experiment

We found a significant year * treatment * location interaction when aboveground biomass ($F_{14,119} = 3.7$; $P < 0.0001$) and grazing intensity ($F_{14,179} = 5.6$; $P < 0.0001$) were entered as dependent variables. To identify the variation associated with each term in this interaction we analyzed each location and year separately. In 1996, aboveground biomass was lower across all locations in plots that had been clipped the previous year (all P values < 0.0003)(Fig. 1a-c). In all locations, AC and DC treated plots differed from those of stable and dynamic control plots. There was over 5 times more aboveground biomass in stable control plots than in AC and DC plots when averaged across all locations. Neither aboveground biomass nor grazing pressure tended to differ between dynamic and stable control plots; however, dynamic control plots were intermediate between stable controls and clipped treatments in 1996 (Fig. 1a-c). Grazing pressure was substantially higher on the AC and DC treated plots across all locations in the 1996 growing season (all P values < 0.0001) (Fig 1a-c). Grazing pressure was lowest on the stable control plots, which when averaged across all locations contained 1 faeces m^{-2} compared to 4 faeces m^{-2} in dynamic controls, and 27 and 25 faeces m^{-2} in AC and DC treatment plots, respectively.

Grazing pressure was lower in 1997 than in 1996 due to a ocean storm surge that inundated portions of the colony (see below). Faecal counts tended to be higher in the AC and DC treatments when compared to the stable and dynamic controls across all locations in 1997 (all P values < 0.0001) (Fig 2a-c). Aboveground biomass was higher in both AC and DC treatments in 1997 when compared to 1996 (Fig 2a-c). The negative relationship between faecal density and aboveground biomass was weaker in 1997 (r^2 = 0.11; $P = 0.049$) than in 1996 ($r^2 = 0.49$; $P < 0.0001$). We did not sample vegetation in 2 of the 3 locations in 2000 because vegetation in the manipulated and dynamic control plots did not visibly differ from the surrounding *C. ramenskii* meadows. However, 5 years after the treatments were applied, there were differences in standing biomass and grazing intensity at 1 of the 3 locations where geese had maintained swards as grazing lawns (Fig 3).

NAPP did not differ among treatments while geese were incubating ($F_{3,11} = 2.3$; $P = 0.18$), or throughout the brood rearing period of 1996 ($F_{3,11} = 0.09$; $P = 0.97$) (Table 1). *NAPP* tended to be lower in both AC and DC treatment plots than in both stable and dynamic controls throughout the 1997 growing season (Table 1). However, *NAPP* did not vary statistically during the late brood rearing period in 1997 ($F_{3,11} = 1.11$; $P = 0.35$).

We found a significant year * treatment interaction when nitrogen-, carbon-concentration, and C:N ratio of *C. ramenskii* sampled at the end of the growing seasons were entered as dependent variables (all P values < 0.001). Therefore, years were analyzed separately. In 1996, *C. ramenskii* in the AC and DC treated plots had both a higher nitrogen concentration and lower C:N ratio than both controls (overall treatment

P values < 0.007) (Table 2). Nutritional characteristics of *C. ramenskii* tended not to differ among treatments in 1997. Vegetation in the treated plots had a higher nitrogen concentration and lower C:N ratios in 2000 when compared to control plots (Table 2).

Estimating the number of families reared from the Tutakoke river colony

The number of families reared from the Tutakoke colony increased from 885 in 1987 to 4165 in 1991 (Fig. 4a). Between 1991 and 1996 the number of families reared from Tutakoke was relatively constant, fluctuating by approximately 400 broods. In 1997 a storm surge of the Bering Sea inundated a large portion of the Tutakoke colony when geese were laying eggs. This, coupled with greater than average arctic fox (*Alopex lagopus*) predation resulted in low nesting success and a 61% decrease in the number of families using brood rearing areas in 1997 than in 1996 (Fig. 4a). Estimates of the number of Brant nests occurred prior to the storm surge. Similarly, we observed a reduction in the number of broods in 1998 when compared to the mid-1990's. We relate this reduction to the effects of abiotic disturbances in the *Discussion* below. By 2000 the population of Brant nesting at Tutakoke had increased to 7437 ± 584 (Fig. 4a).

Changes in the zonation of plant communities

The areal extent of *C. subspathacea* increased from 2.9 ± 0.6 to 8.3 ± 0.8 % between 1991 and 1999 (overall slope: $P < 0.0001$) (Fig. 4b). In contrast, the areal extent of C. ramenskii-dominated meadows decreased from 30.0 ± 4.9 to 27.1 ± 2.0 % over the same time period (overall slope: $P = 0.001$). We tested the inverse relationship between these regression models by comparing the absolute value of their slopes and failed to detect a difference ($Z = 0.24$, $P > 0.5$), suggesting a large scale inter-conversion between the two

community types. The areal extent of the slough levee community ranged in cover from 19.3 ± 2.7 % in 1991 to 21.1 ± 1.9 % in 1999 (Fig.4b). Mudflats, lakes, and tidal rivers and sloughs comprise approximately 50% of the 10 km^2 Tutakoke colony landscape (Table 3).

Changes in gosling mass

Between 1987 and 1998 we marked and subsequently recaptured 1302 known-age goslings on a sample of brood rearing areas. Gosling mass varied among years ($F_{11,1174}$ = 1.95; P = 0.029) (Fig. 4c). Goslings were largest when the number of families reared from the Tutakoke colony was first beginning to recover from harvest and predation pressures in the late 1980's (Fig. 4c). Gosling mass steadily declined from 810 to 590 g between 1989 to 1992 coincident with the stabilization of the number of broods produced from the Tutakoke colony. In contrast, gosling mass increased 100 g between 1992 and 1998 (Fig. 4c) despite observing density dependent features in population size (Fig. 4a).

Feedbacks between herbivore density, grazing lawn extent, and gosling mass

We regressed the lagged extent of grazing lawn on the number of broods to examine the effect of herbivore population size on the areal extent on grazing lawns within the Tutakoke River landscape. We used a four year lagged relationship between the extent of grazing lawn and brood density because we believe there is a disparity between changes in goose density and the rate at which these changes can drive landscape increases in grazing lawn extent. We found a positive relationship between these two variables (y = 1.75 (x) + 0.09; r^2 = 0.63: $P < 0.001$). Similarly, we examined

the relationship between grazing lawn extent and gosling mass between 1991 - 1999 and found a positive relationship between these variables ($r^2 = 0.36$) (Figure 5).

Discussion

Removing aboveground tissues of *C. ramenskii*, whether by mowing or grazing, results in a sward that Brant prefer to graze and can maintain as a grazing lawn. On the sward scale (*e.g.*, 225 m^2) the resulting lawn attains a prostrate growth form that is morphologically and nutritionally indistinguishable from a *C. subspathacea* grazing lawn (Fig. 6). Given that these sedges were once classified as the same species, the ecological evidence presented here indicates that genetically characterizing these morphological types is warranted. Person et al. (1998) reported *C. subspathacea* aboveground biomass ranged from 18 to 81 g m^{-2} in mid-July across several landscapes used by broods from the Tutakoke colony in 1994 and 1995. Here we report that when heavily grazed, aboveground biomass of *C. ramenskii* ranged from 9 to 72 g m^{-2}. The nutritional quality of grazed *C. ramenskii* is also similar to that of *C. subspathacea*. C:N ratios range from 19 to 8 for grazed *C. ramenskii* and from 20 to 11 for *C. subspathacea* (Person et al. 1998). Thus, under high grazing pressures these sedges appear to converge in their nutritional characteristics as well as growth forms.

This shift in character state of *C. ramenskii* is bi-directional. For instance, in an unrelated experiment we fenced swards of *C. subspathacea* that had an average biomass of 14 ± 1.5 g dwt m^{-2} in 1994. Following three years of protection from grazing these swards had 369 ± 74 g dwt m^{-2} standing biomass and 299 ± 80 g dwt m^{-2} standing dead

compared to no standing dead within grazed control *C. subspathacea* lawns that had a mean SCB of 16 ± 4 g dwt m^{-2}. During the winter of 1997-98 these exclosures were removed, thereby allowing geese to freely choose to feed on the tall character state vegetation within these plots. Geese grazed vegetation in these plots, which resulted in a SCB that averaged 18 ± 2 g dwt m^{-2} in 2001. Similarly, the combined influences of the spring storm surge and above-average arctic fox predation in 1997 resulted in a 61% decrease in the number of families using brood rearing areas when compared to 1996. The consequent decrease in grazing pressure allowed vegetation in our manipulated plots to revert to the tall *C. ramenskii* growth form at some locations.

Coughenour (1985) suggested that grazing lawns are created through phenotypic plasticity or ecotypic differentiation within local plant populations subjected to chronic grazing pressures, and Painter et al. (1993) found evidence of both phenotypic plasticity and ecotypic differentiation within a landscape grazed by prairie dogs (*Cynomys ludovicianus*). Grazing tolerant ecotypes retain their morphology when protected from grazing for several growing seasons (Carmen and Briske 1985; Painter et al. 1989) while phenotypically plastic species rapidly change character states in response to herbivory (McNaughton 1984; Stearns 1992; Painter et al. 1993). Thus, a fundamental distinction exists, in that grazing lawns dominated by ecotypes should buffer a food web against disturbances that remove or reduce consumers from a system for a short period. In contrast, a plastic response of vegetation to the removal of consumers likely introduces time lags in feedbacks between consumer-induced changes in the structure of a food web, and the subsequent numerical response of the herbivore population.

The character state of *C. ramenskii* can shift rapidly in response to the addition or removal of grazing pressure, indicating that this sedge expresses phenotypic plasticity (McNaughton 1984; Stearns 1992; Painter et al. 1993). However, throughout the Tutakoke colony we observe patchy assemblages of the two character states under both high and low grazing pressures. We offer two hypotheses, which are not mutually exclusive, for the existence of these assemblages. First, variation in microtopography and edaphic characteristics may influence the growth form and nutritional quality of *C. ramenskii*, to which Brant respond by grazing some patches more than others. This creates an assemblage of grazed hot-spots and patches of ungrazed *C. ramenskii.* Trampling and soil compaction by geese lead to soil conditions that favor the short growth form. Ruess et al. (1997) described a feedback between the effects of trampling along trails frequently traveled by Brant and the dominance and subsequent use of the short growth form along these trails. We observed a similar response in an unrelated experiment where human trampling near experimental plots within a *C. ramenskii* meadow induced a character state shift from the tall- to short-morphology which Brant discovered and maintained as a grazing lawn.

Our second hypothesis is that the resistance of some patches of *C. ramenskii* to change character states under high and low grazing pressures is due to ecotypic variation throughout the distribution of *C. ramenskii* (Carmen and Briske 1985; Coughenour 1985; Painter et al. 1989; Painter et al. 1993). One of these ecotypes exists primarily along coastal fringes where both salinity and historic grazing pressure have been high, even at low population densities. The phenotypic plasticity of these "permanently short"

ecotypes is relatively low, perhaps constrained by environmental stress. However, the majority of *C. ramenskii* occurs in more inland sites where environmental stress and grazing pressures are lower (Ruess et al. 1997). The plasticity of these ecotypes is high. We suggest the resilience (*i.e.*, phenotypic plasticity) of *C. ramenskii* to grazing pressures is variable throughout its distribution, and character states are partially dependent on a coupling of defoliation history and edaphic characteristics (*i.e.*, ecotypic variation). When grazing pressure is high, Brant create a grazing lawn of *C. ramenskii* that doesn't differ structurally or functionally from *C. subspathacea* swards.

An important feature of this system is that the behaviour of Brant allows them to create and maintain grazing lawns even during years of low population abundance. McNaughton (1984) hypothesized that it is only in herds that herbivores can create and maintain grazing lawns. Brant maintain 'herds' that are independent of overall population size, but it is the collective effects of these family groups that drive landscape changes in grazing lawn distribution.

Growth of goslings is sensitive to variation in *per capita* forage availability and quality, and the nutritional environment goslings experience affects survival, final body size, and future fecundity (Cooch et al. 1991; Larsson and Forslund 1991; Sedinger and Flint 1991; Lindholm et al. 1994). Gosling mass was greatest when the population of Brant breeding at Tutakoke was low in the late-1980's, and decreased as the population began to recover from harvest and predation pressures (Fig 4c). However, gosling mass increased between 1992 and 1998 concurrent with population estimates that are characteristic of a population which has reached carrying capacity (Fig. 4a). We attribute

the recent increase in gosling mass to the associated feedbacks between herbivory and grazing lawn zonation.

Because size of young is a strong determinant of recruitment and future fecundity, we believe the interplay between population size and the areal extent of grazing lawns will result in a numeric increase in this population. But, such a population response is subject to time lags. For example, fewer goslings reared during the early 1990's will breed, and those recruited into the breeding population will produce fewer offspring because these cohorts consisted of small goslings. Breeding probability for individuals that are recruited into the population is a function of size (J. S. Sedinger unpublished data). Similarly, breeding propensity, clutch size, and age at first breeding are positively correlated with female body size in Brant (Sedinger et al 1995). Furthermore, individuals do not reach peak breeding probability until they are four years old because clutch size is reduced until this age (Sedinger et al. 1995).

Variation associated with climatic and biotic disturbances, like those that reduced the number of families reared from Tutakoke in 1997, will delay detection of an increase in the population. Cross-latitudinal effects on the wintering grounds, such as those that reduced all breeding Brant populations by approximately 20% in 1998 (D. H. Ward pers. comm.), would also affect the rate of a numerical response of Brant to changes in the extent of grazing lawns. Thus, we predict that the herbivore-mediated changes in plant community zonation observed between 1991 and 1999 will impact the size of the Brant population breeding at Tutakoke within one to two decades. We do not suggest that the feedbacks we've described are the only factor that regulates this population. However,

the feedbacks between population size, grazing lawn extent, and the subsequent effects on gosling size likely contribute, in part, to the regulation of the carrying capacity of these breeding grounds.

Our data contrast with goose-vegetation dynamics in the eastern Canadian subarctic where increasing populations of lesser snow geese (*Anser c. caerulescens*) have destroyed vast expanses of *C. subspathacea* and *Puccinellia phryganodes* grazing lawns along the Hudson and James Bay coast (Kerbes et al. 1990). The expansion of this population has resulted from a coupling of changes in land-use patterns in lower latitudes with over-winter subsidies in the diet of lesser snow geese. Destruction of breeding-ground habitat is the principal result of spring grubbing for belowground tissues, a foraging behaviour not exhibited by Brant. Lesser snow goose gosling growth and survival declined coincident with increases in goose density and decline in habitat (Cooch et al. 1993). In contrast, we report an increase in gosling mass over the past decade (Figure 4c). When preferred food resources are limiting, Brant and lesser snow geese are forced to select alternative foods to maintain a positive energy and nitrogen balance because both species demonstrate intra- and interannual faithfulness to brood rearing areas (Cooch et al. 1993; Lindberg and Sedinger 1998). Lesser snow geese switch from *C. subspathacea* and *P. phryganodes* grazing lawns to forage species lower in quality and less tolerant of grazing (Zellmer et al. 1993; Gadallah and Jefferies 1995). Differences in the foraging ecology of these goose species, coupled with isostatic rebound of the region, hypersalinization of soils are the most marked differences between these two colonies (Gadallah and Jefferies 1995; Srivastava and Jefferies 1995). Increased grazing pressure

by lesser snow geese has led to the collapse of an ecosystem. In contrast, increases in Brant grazing pressure has had a positive effect on the creation and maintenance of grazing lawns along the Bering Sea coast.

The plastic response to herbivory by *C. ramenskii* offers a mechanism through which this ecosystem shifts between alternate states. We believe there was a state shift of this system when the Brant population declined from 7400 to 1100 pairs. The corresponding decrease in grazing pressure likely resulted in a reduction in the areal extent of grazing lawns due to the plastic response of *C. ramenskii*. As the population increased, it experienced density dependent effects and was controlled by bottom-up forces (*e.g.*, grazing lawn extent) between 1989 – 1992 (Sedinger et al. 1998). After 1992, we observed an increase in mass of goslings reared from the Tutakoke colony despite a population structure that appears to have equal birth and death rates. We believe that bottom-up forces no longer control the Tutakoke population. Rather, we have observed strong top-down control of this system over the past six years. Specifically, we suggest grazing by Brant has increased the areal extent of grazing lawns. We suggest that bottom-up forces in this ecosystem occur at an annual time scale due to the high plasticity of *C. ramenskii*, and that top-down control by Brant occurs on the order of decades. Thus, the long-term carrying capacity of this ecosystem is likely higher than current population estimates of Brant breeding at Tutakoke reflect. These data emphasize the importance of understanding the stochasticity of population dynamics when evaluating the assumption of density dependence in a population.

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References

Anthony RM, Flint PF, Sedinger JS (1991) Arctic fox removal improves nesting success of Black Brant. Wildl Soc Bull 19:176-184.

Anthony RM, Anderson WH, Sedinger JS, McDonald LL (1995) Estimating populations of nesting Brant using aerial videography. Wildl Soc Bull 23: 80-87.

Anthony RM (2001) Aerial videography of brant colonies on the Yukon Delta NWR in 2000. Report to Pacific Flyway Council. U.S. Geological Survey, Alaska Biological Science Center, Anchorage, Alaska, USA.

Bazely DR, Jefferies RL (1985) Goose faeces: a source of nitrogen for plant growth in a grazed marsh. J Ecol 22:693-703.

Bazely DR (1986) Changes in the composition and standing crop of salt marsh communities in response to removal of a grazer. J Ecol 74:693-706.

Bellrose FC (1980) Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania.

Buchsbaum R, Wilson J, Valiela I (1986) Digestibility of plant constituents by Canada geese and Atlantic Brant. Ecology 67:386-393.

Carmen JG, Briske DD (1985) Morphologic and allozymic variation between long-term grazed and non-grazed populations of the bunchgrass *Schizachyrium scoparium* var. *frequens*. Oecologia 66:332-337.

Cooch EG, Lank DB, Duzbin A, Rockwell RF, Cooke F (1991) Body size variation in Lesser Snow Geese: seasonal variation in gosling growth rate. Ecology 72:503-512.

Cooch EG, Jefferies RL, Rockwell RF, Cooke F (1993) Environmental change and the cost of phylopatry: an example in the lesser snow geese. Oecologia 93:128-138.

Coppock DL, Detling JK, Ellis JE, Dyer MI (1983a) Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of Black-Tailed Prairie Dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56: 1-9.

Coppock DL, Detling JK, Ellis JE, Dyer MI (1983b) Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of Bison to modification of vegetation by Prairie Dogs. Oecologia 56: 10-15.

Coughenour MB (1985) Graminoid responses to grazing by large herbivores: adaptation, exaptations, and interacting processes. Annals of the Missouri Botanical Garden 72:852-863.

Coughenour MB, Singer FJ (1996) Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecol Appl 6: 573-593.

Demment MW, VanSoest PJ (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. Amer Nat 125: 641-672.

East R (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. Afr J Ecol 22:245-270.

Gadallah FL, Jefferies RL (1995) Comparison of the nutrient contents of the principal forage plants utilized by lesser snow geese on summer breeding grounds. J Appl Ecol 32:263-275.

Gill RE Jr., Handel CM (1990) The importance of subarctic intertidal habitats to shorebirds: A study of the Yukon-Kuskokwim Delta, Alaska. Condor 92:709-725.

Hik DS, Jefferies RL (1990) Increases in the net above-ground primary production of a salt marsh forage grass: a test of the predictions of the herbivore-optimization model. J Ecol 78:180-195.

Hobbs NT, Swift DM (1985) Estimates of habitat carrying capacity incorporating explicit nutritional constraints. J Wildl Manag 49: 814-822.

Hughes JR, Reed A, Gauthier G (1994) Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. J Wildl Manag 58: 536-545.

Hultén E (1941) Flora of Alaska and Yukon,1-10. Lunds Universitets. Årsskrift N.F.

Hultén E (1990) Flora of Alaska and neighboring territories. A manual of the vascular plants. Stanford University Press, Stanford, California.

Jefferies RL, Klein DR, Shaver GR (1994) Vertebrate herbivore and northern plant communities reciprocal influences and responses. Oikos 71:193-206.

Kerbes RH, Kotanen PM, Jefferies RL (1990) Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. J Appl Ecol 27:242-258.

King JG, Derksen DV (1986) Alaska goose populations: past, present, and future. Transactions of North American Wildlife Conference 51:464-479.

Larsson K, Forslund P (1991) Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. J Evol Biol 4:679-686.

Lieff BC (1973) Summer feeding ecology of Blue and Canada geese at the McConnel River, N.W.T. Unpublished Ph.D. dissertation. London, Ontario, Univ Western Ontario.

Lindberg MS, Sedinger JS (1998) Ecological significance of brood-site fidelity in Black Brant: Spatial, annual, and age-related variation. Auk 115:436-446.

Lindholm A, Gauthier G, Desrochers A (1994) Effects of hatch date and food supply on gosling growth in arctic-nesting Greater Snow Geese. Condor 96:898-908.

McNaughton SJ (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92-94.

McNaughton SJ (1983) Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecol Mono 53:291-320.

McNaughton SJ (1984) Grazing lawns: Animals in herds, plant form, and coevolution. Amer Nat 124:863-886.

McNaughton SJ (1985) Ecology of a grazing ecosystem: The Serengeti. Ecol Mono 55:259-294.

McNaughton SJ, Banyikwa FF, McNaughton MM (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798-1800.

Mitchell SF, Wass RT (1996) Quantifying herbivory: grazing consumption and interaction strength. Oikos 76:573-576.

Mulder CPH, Ruess RW, Sedinger JS (1996) Effects of environmental manipulations on *Triglochin palustris*: implications for the role of goose herbivory in controlling its distribution. J Ecol 84:267-278.

Mulder CPH, Ruess RW (1998) Effects of herbivory on arrowgrass: interactions between geese, neighboring plants, and abiotic factors. Ecol Mono 62:275-293.

Oesterheld M, Sala OE, McNaughton SJ (1992) Effect of animal husbandry on herbivore-carrying capacity at a regional scale. Nature 356:234-236.

Painter EL, Detling JK, Steingraeber DA (1989) Grazing history, defoliation, and frequency-dependent competition: effects on two North American grasses. Amer J Bot 76:1368-1379.

Painter EL, Detling JK, Steingraeber DA (1993) Plant morphology and grazing history: relationships between native grasses and herbivores. Vegitatio 106:37-62.

Pastor J, Naiman RJ (1992) Selective foraging and ecosystem processes in boreal forests. Amer Nat 139:690-705.

Pastor J, Cohen Y (1997) Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. Theor Popul Biol 51, 165-179.

Pastor J, Moen R, Cohen Y (1997) Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. J Mamm 78:1040-1052.

Person BT, Babcock CA, Ruess RW (1998) Forage variation in brood-rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska. J Ecol 86: 243-259.

Poole RW (1974) An introduction to quantitative ecology. McGraw-Hill, New York.

Raveling DG (1986) Geese hunters of Alaska's Yukon-Kuskokwim Delta: management problems and political dilemmas. Transactions of North American Wildlife and Natural Resource Conference 49:555-575.

Raveling DG (1989) Nest-predation rates in relation to colony size of Black Brant. J Wildl Manag 53:87-90.

Ricklefs RE (1973) Patterns of growth in birds. Growth rate and mode of development. Ibis 115:177-201.

Ruess RW, Hik DH, Jefferies RL (1989) The role of Lesser Snow Geese as nitrogen processors in a sub-arctic salt marsh. Oecologia 79:23-29.

Ruess RW, Uliassi DD, Mulder CPH, Person BT (1997) Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: Implications for geese-ecosystem dynamics in western Alaska. EcoScience 4:170-178.

SAS Institute Inc. 1990. SAS/STAT *User's Guide*, Release 6.04 edition. SAS Institute Inc., Cary, North Carolina.

Sedinger JS, and Raveling DG (1984) Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295-306.

Sedinger JS, Raveling DG (1988) Foraging behavior of cackling canada goose goslings: implications for the roles of food availability and processing rate. Oecologia 75:119-124.

Sedinger JS, Flint PF (1991) Growth rate is negatively correlated with hatch date in Black Brant. Ecology 72:496-502.

Sedinger JS, Lensink CJ, Ward DH, Anthony RM, Wege ML, Byrd GV (1993) Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. Wildfowl 44:49-59.

Sedinger JS, Flint PF, Lindberg MS (1995) Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404-2414.

Sedinger JS (1996) Geese of the Yukon-Kuskokwim delta: Improvements or illusions? *in* Seventh International Waterfowl Symposium (*Ed.* Ratti, J. T.), Ducks Unlimited, Memphis, Tennessee.

Sedinger JS (1997) Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99:314-326.

Sedinger JS, Lindberg MS, Person BT, Eichholz MW, Flint PL (1998) Density-dependence effects on growth, body size, and clutch size in black brant. Auk 115:613-620.

Singer FJ, Harting A, Symonds KK, Coughenour MB (1997) Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. J Wildl Manag 61: 12-25.

Spencer DL, Nelson UC, Elkins WA (1951) America's greatest goose-brant nesting area. Transactions of North American Wildlife Conference 16:290-295.

Srivastava DS, Jefferies RL (1995) Mosaics of vegetation and soil salinity: a consequence of goose foraging in an arctic salt marsh. Can J Bot 73:75-83.

Stearns SC (1992) The evolution of life histories. Oxford University Press, New York.

Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark-bellied brent *Branta b. bernicla* (L.) in relation to food depletion. Oecologia 103: 499-508.

Zar HH (1996) Biostatistical Analyses. Simon and Shuster, Upper Saddle River, New Jersey.

Zellmer ID, Clauss MJ, Hik DS, Jefferies RL (1993) Growth responses of arctic graminoids following grazing by captive lesser snow geese. Oecologia 93:487-492.

Table 3.1. Mean net aboveground primary productivity (*NAPP*) of *Carex ramenskii* from the *Mowing experiment* conducted at the Tutakoke River black brant colony on the Yukon-Kuskokwim Delta, Alaska during the 1996 and 1997 growing seasons. Results are from ANOVA, Tukey's HSD method. Letters shared within columns are not statistically different at alpha = 0.05. Values represent mean ± SE g dwt m^{-2} d^{-1}.

	NAPP DURING INCUBATION		*NAPP* DURING BROOD REARING		*NAPP* DURING LATE BROOD REARING
TREATMENT	1996	1997	1996	1997	1997
STABLE CONTROL	5.4 ± 1.2 a	2.5 ± 0.2 ab	-0.1 ± 1.6 a	6.3 ± 0.8 a	4.9 ± 1.3 a
DYNAMIC CONTROL	5.2 ± 0.8 a	1.6 ± 0.3 b	2.7 ± 1.5 a	6.8 ± 0.9 a	4.2 ± 1.6 a
ADJACENT CLIPPED	4.1 ± 0.5 a	2.2 ± 0.2 ab	2.7 ± 1.4 a	3.2 ± 0.7 b	2.3 ± 0.7 a
DISTANT CLIPPED	3.8 ± 0.5 a	2.9 ± 0.4 a	3.6 ± 0.9 a	3.8 ± 0.6 ab	4.3 ± 1.6 a

Table 3.2. Treatment differences in carbon and nitrogen concentration and the carbon to nitrogen ratio (C:N) of *Carex ramenskii* harvested at the end of the 1996-97 and 2000 growing seasons. Letters shared within columns and years do not differ statistically at alpha = 0.05 (Tukey's HSD). Treatment codes are: Stable control (S.CTL), dynamic control (D.CTL), adjacent clipped (AC), and distant clipped (DC) plots. Data are means ± 1 SE.

		NUTRITIONAL CHARCTERISTICS		
YEAR	TREATMENT	CARBON	NITROGEN	C : N
1996	S.CTL	43.5 ± 0.2 a	1.8 ± 0.1 a	24.2 ± 0.6 ab
	D.CTL	44.2 ± 0.1 a	1.8 ± 0.1 a	24.7 ± 0.8 a
	AC	43.7 ± 0.3 a	2.5 ± 0.2 b	18.6 ± 1.3 bc
	DC	40.6 ± 1.1 a	2.8 ± 0.1 b	14.5 ± 0.9 c
1997	S.CTL	43.9 ± 0.1 a	1.8 ± 0.4 a	24.3 ± 0.6 a
	D.CTL	44.0 ± 0.1 a	1.8 ± 0.1 a	24.9 ± 0.6 a
	AC	43.6 ± 0.1 ab	1.9 ± 0.1 a	23.9 ± 1.4 a
	DC	43.5 ± 0.2 b	1.9 ± 0.1 a	24.0 ± 1.1 a
2000	S.CTL	44.7 ± 1.9 a	1.8 ± 0.1 a	24.8 ± 1.6 a
	D.CTL	48.6 ± 3.6 a	2.2 ± 0.2 a	22.6 ± 1.8 a
	AC	43.5 ± 0.2 a	4.0 ± 0.4 b	11.3 ± 1.0 b
	DC	43.7 ± 0.3 a	4.4 ± 0.3 b	10.2 ± 0.8 b

Table 3.3. Percent cover of the dominant physiographic features at the Tutakoke River black brant colony on the Yukon-Kuskokwim Delta, Alaska.

	Physiographic Features			
Year	Mud	Lake	River / Slough	Other
1991	31.2 ± 5.0	13.5 ± 3.1	3.1 ± 0.8	$7.6e^{-3} \pm 5.3e^{-3}$
1993	29.9 ± 5.1	12.9± 3.0	5.4 ± 1.4	$3.0e^{-2} \pm 2.0e^{-2}$
1994	30.4 ± 5.3	11.1 ± 2.6	3.7 ± 1.5	$1.2e^{-2} \pm 7.4e^{-3}$
1995	32.5 ± 5.8	14.3 ± 3.2	2.5 ± 0.9	0.2 ± 0.1
1997	32.2 ± 5.8	12.4 ± 3.1	6.0 ± 1.8	$5.3e^{-2} \pm 3.0e^{-2}$
1998	26.2 ± 2.4	15.1 ± 1.6	5.1 ± 1.2	0.6± 0.02
1999	22.8 ± 2.0	10.1 ± 1.2	10.8 ± 1.5	0.8± 0.02

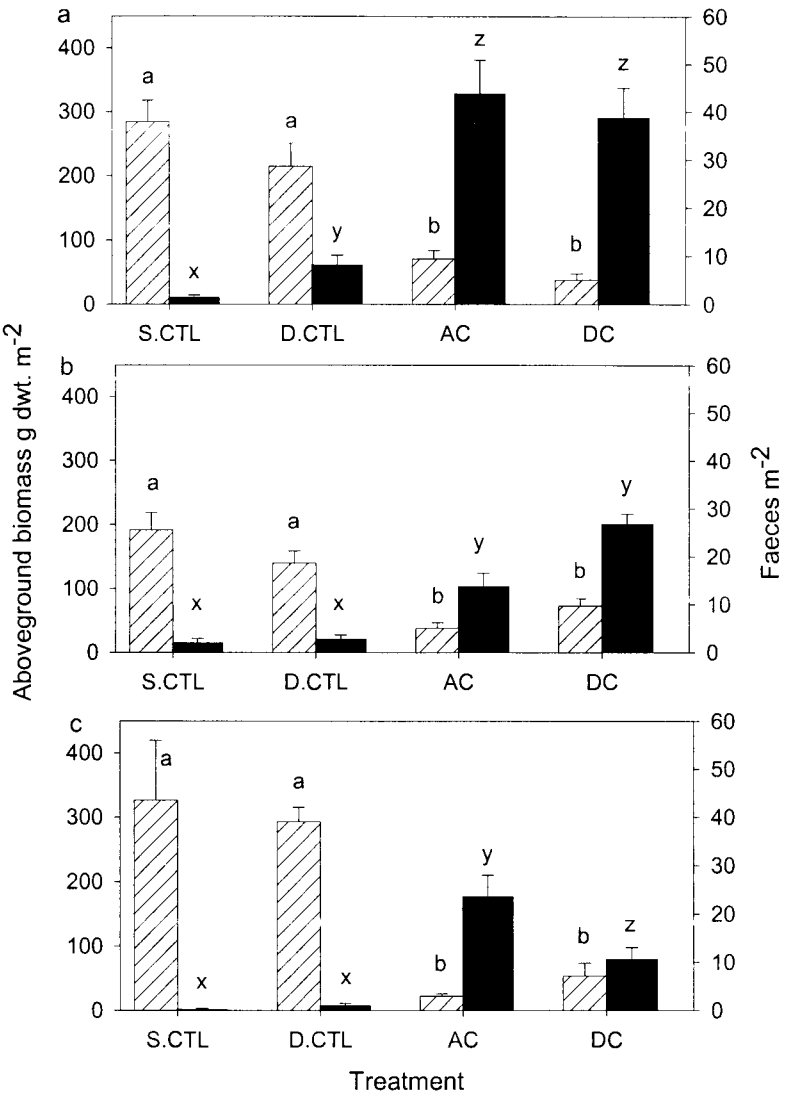

Figure 3.1. Treatment differences in aboveground biomass and grazing intensity, as indexed by faecal counts, at the end of the 1996 growing season. Data follow mowing treatments applied one year earlier to the *Carex ramenskii* community at three locations within the Tutakoke River Brant colony on the Yukon-Kuskokwim Delta, AK. We detected a significant year * location * treatment interaction when each aboveground biomass and grazing intensity were entered as dependent variables, hence Figure **1 (a)** corresponds to location 1, **(b)** location 2, and **(c)** location 3. Hatched-bars represent aboveground biomass and solid-bars grazing intensity. Treatment abbreviations are as follows: S. CTL = stable control (tall form *C. ramenskii*); D. CTL = dynamic control (grazed 'hot spots'); AC = clipped treatment adjacent to the dynamic control; DC = clipped treatment approximately 150 m distant from the AC treatment plots. Data represent means ± SE. Letters shared between treatments, for corresponding bar fills, represent Tukey's honest significant difference (HSD) multiple comparisons and are not different at alpha > 0.05

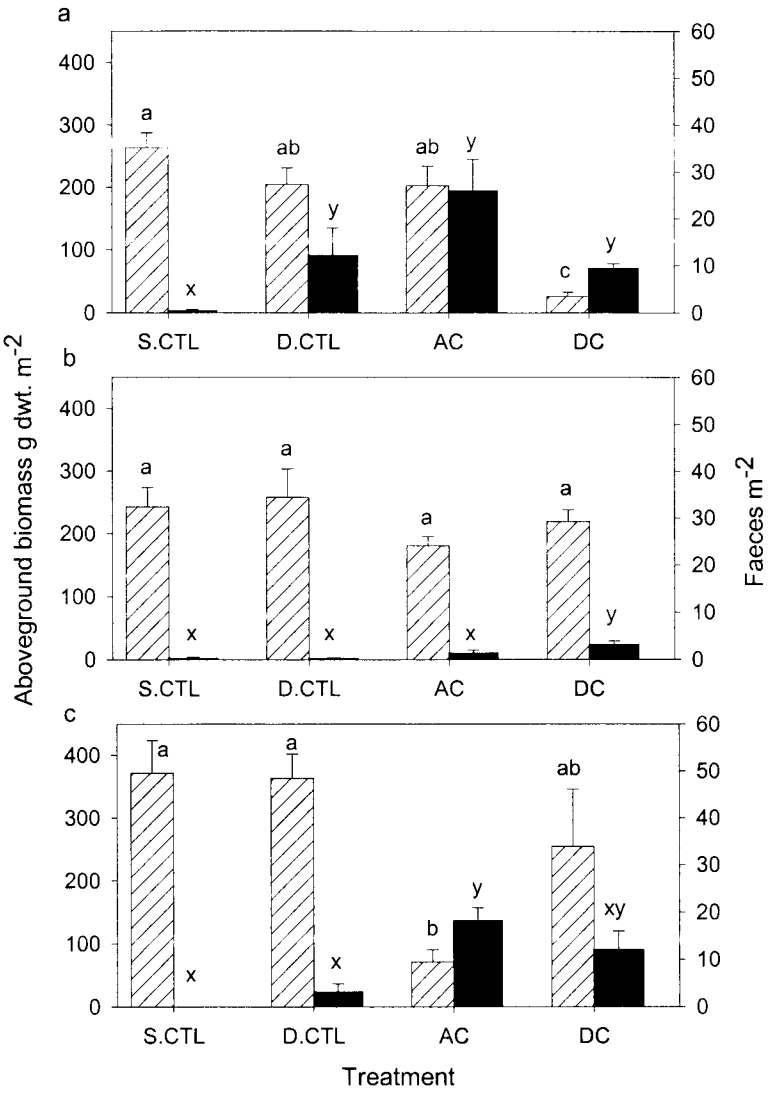

Figure 3.2. Treatment differences in aboveground biomass and grazing intensity, as indexed by faecal counts, at the end of the 1997 growing season. Data follow mowing treatments applied two years earlier to the *Carex ramenskii* community at three locations within the Tutakoke River Black Brant colony on the Yukon-Kuskokwim Delta, AK. Bar fills and treatment abbreviations follow figures **1 a – c**. Data represent means ± SE. Letters shared between treatments, for corresponding bar fills, represent Tukey's HSD multiple comparisons and are not different at alpha > 0.05.

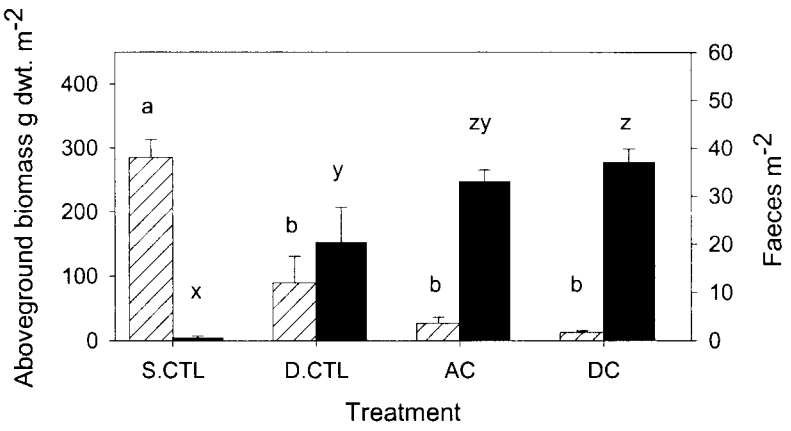

Figure 3.3. Treatment differences in aboveground biomass and grazing intensity, as indexed by faecal counts, at the end of the 2000 growing season. Data follow mowing treatments applied five years earlier to the *Carex ramenskii* community at 1 of the 3 locations within the Tutakoke River Black Brant colony on the Yukon-Kuskokwim Delta, AK. Vegetation in location 1 and 2 did not visibly differ from the surrounding *C. ramenskii* meadows therefore we did not sample it or grazing intensity. Bar fills and treatment abbreviations follow figures 1 a – c. Data represent means ± 1 standard error. Letters shared between treatments, for corresponding bar fills, represent Tukey's HSD multiple comparisons and are not different at alpha > 0.05.

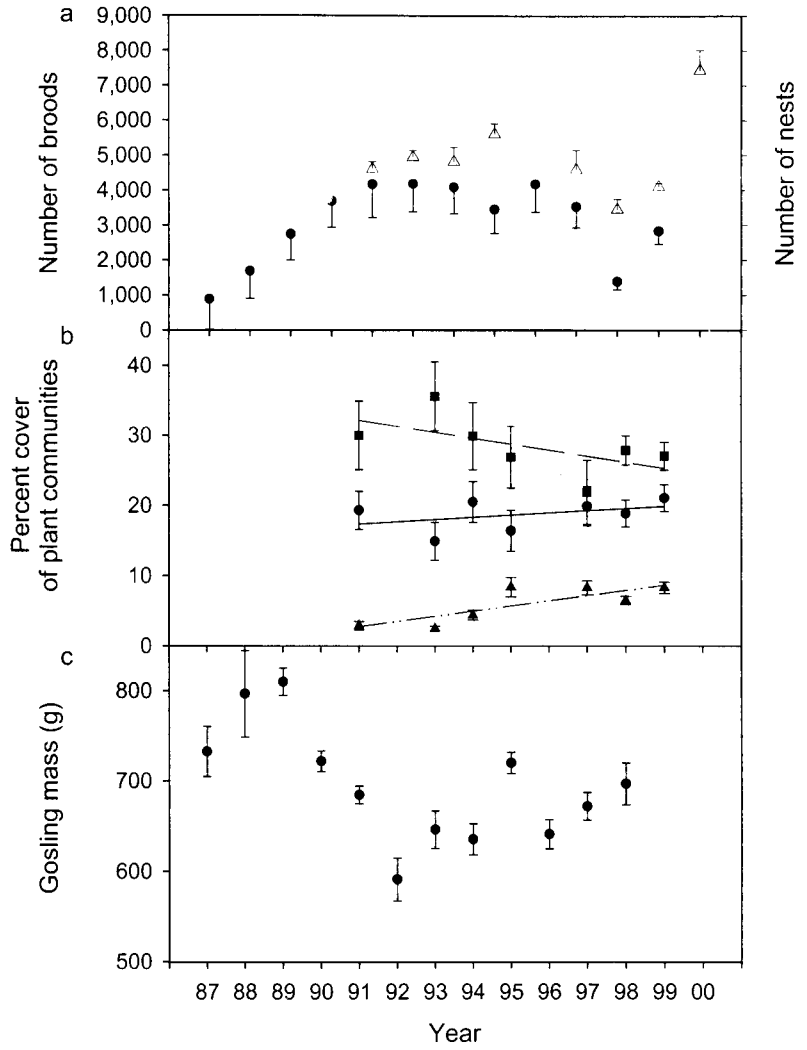

Figure 3.4 (a). Lincoln-Peterson estimates (●) of the number of black brant families using brood-rearing areas on which adults and goslings reared from the Tutakoke River colony were recaptured and weighed between 1987 – 1998, data represent mean ± SE. Number of Brant nests (△) 2 – 3 weeks prior to mean hatch between 1991 – 2000. Nest density was estimated using areal videography techniques, data represent mean ± SE. **(b)** Changes in the percent coverage of the three community types comprising the Tutakoke River Black Brant colony on the Yukon-Kuskokwim Delta, AK. Symbols are as follows: ■ *Carex ramenskii* dominated meadows; ● slough-levee community; ▲ *C. subspathacea* grazing lawns. Lines were fitted using linear regression on arcsine transformed data. Aerial extent of *C. ramenskii*-meadows declined ($y = -0.014\ (x) + 1.75$; $P = 0.001$) concurrent with an increase in *C. subspathacea* community ($y = 0.007\ (x) - 0.63$; $P \leq 0.0001$). The slough levee community increased slightly throughout this period ($y = 0.01\ (x) - 1.73$; $P = 0.014$) **(c)** Changes in known-age gosling mass over years in which population density and aerial coverage of plant communities comprising the Tutakoke River colony were changing. Symbols represent least squared means ± SE after controlling for sex, age, and year differences.

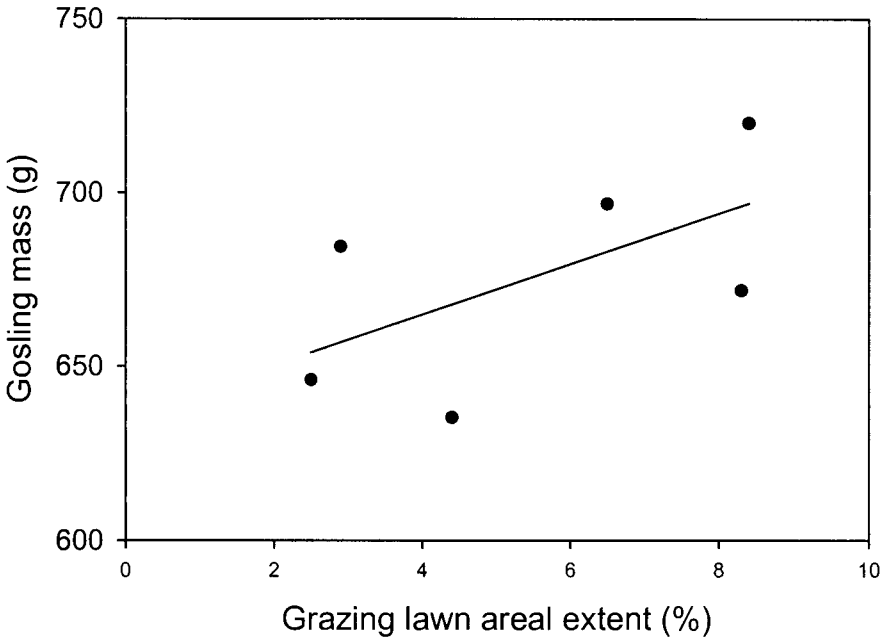

Figure 3.5. The relationship between gosling mass (least square mean) and areal extent of grazing lawns (%) within the Tutakoke River colony between 1991 - 1999 ($y = 635 (x) + 7.3$; $r^2 = 0.36$).

Figure 3.6. A grazing lawn that was created 5 years earlier by mowing and removing aboveground tissues of *C. ramenskii*. Vegetation in the foreground is an example of *C. ramenskii* that is in a short morphology, it is indistinguishable from *C. subspathacea*. The exclosure in the center of the photograph was not manipulated in 1995 and is representative of the tall-ungrazed morph of *C. ramenskii* that dominated this area prior to treatment application. This is one of the DC treatment plots at location 3.

CHAPTER 4. Stability of a near Arctic saltmarsh: Community resistance to tidal disturbance[4]

Abstract: Coastal ecosystems are likely to experience increased tidal disturbance in response to global climate change through a coupling of increased storm activity and the melting of ice reserves in northern latitudes. The Yukon-Kuskokwim Delta, in southwestern Alaska, is an important ecosystem for investigating the impact increased tidal flooding may have on salt marsh soil processes and plant communities because it is the principle breeding grounds for several populations of geese. We investigated the effect tidal flooding and grazing had on three plant communities known to have important life history consequences for Black Brant (*Branta bernicla nigricans*) geese by flooding these communities with tidal waters in the field. Relative to controls, treatments that were flooded weekly had soils that had doubled, tripled, and increased six fold in salinity in the *C. subspathacea*, *C. ramenskii* meadow, and slough levee communities, respectively. We detected no effect on either soil processes or live plant standing biomass, and growth in the most coastal *C. ramenskii* and *C. subspathacea* communities. Standing crop live biomass in the slough levee community was lower in plots that had soil salinities six times higher than ambient soil salinity. This effect resulted from am 83% decline in woody vegetation. Grass biomass increased in these plots however, and maintained the productivity of this community relative to controls. Grazing did not have

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a strong effect on the structure of the slough levee or *C. ramenskii* communities in this experiment; however, geese reduced the biomass of a preferred forage species (*T. palustris*) by 50% over two growing seasons. Geese removed over 95% of *C. subspathacea* annual aboveground production without any effect on its growth, even in soils that had twice the ambient salinity. Graminoid tissues from the most saline treatments had elevated N concentrations in all communities. We suggest these communities are resistant to short-term tidal disturbance and discuss the potential implications of long-term tidal disturbance in this salt marsh.

INTRODUCTION

Cyclonic storm events in the Bering Sea region are predicted to increase in response to climate change (Walsh *et al.* 1996; Serreze *et al.* 1997). Increased frequency of storm events combined with melting of ice reserves are predicted to increase the extent and frequency of tidal flooding in the coastal zone of the Yukon-Kuskokwim (Y-K) Delta in southwestern Alaska (Wise *et al.* 1981; Sallenger 1983). Increased tidal flooding would likely elevate soil salinities and decrease the redox potentials of soils. Plant standing crop biomass, community diversity, and nutrient uptake by plants have been reduced under these conditions (Rozema & Bloom 1977; Bradly & Morris 1991; Chambers *et al.* 1998; Gough & Grace 1998). Reduction of aboveground biomass would likely impact consumers in this system. The Y-K Delta supports some of the largest and most diverse breeding populations of waterfowl in the circumpolar subarctic (Nudds 1992), including four species of herbivorous geese (Bellrose 1980, Owen 1980). Because

the nutritional environment experienced by goslings affects their final body size, recruitment rate, and future fecundity (Cooch *et al.* 1991, Larsson & Forslund 1991, Sedinger *et al.* 1995), we investigated the effect increased tidal disturbance would have on edaphic and plant community characteristics by flooding three plant communities known to be important to geese breeding in this area.

Increased tidal flooding can affect soil processes and plant community characteristics by elevating soils salinities, and through the depletion of oxygen in flooded soils by plants and soil microbes (Ponnamperuma 1984). Both salinity and inundation pressures can lead to a reduction in soil nitrogen and carbon mineralization rates (Ponnamperuma 1984; Wilson & Jefferies 1996) and decreased efficiency of nutrient uptake by plants (Bradly & Morris 1991; Chambers *et al.* 1998). Similarly, decreased plant growth and survival results from stomatal closure in response to saline conditions. Thus, a trade-off between plant water loss and CO_2 uptake from stomates occurs under saline soil conditions (Jackson & Drew 1984; Wainwright 1984; Neumann 1997). Some plants can ameliorate these pressures through morphological and physiological acclimation to their environment (Brown & Hellebust 1977; Story & Wyn Jones 1977; Jackson & Drew 1984) or through selective pressures within a population (Wainwright 1984; Neumann 1997). Thus, while plants growing in inland (*e.g.*, less tidally influenced) communities are more likely to be negatively effected by tidal disturbance, the increased diversity of inland communities (Bertness 1991; Bertness *et al.* 1992) is likely to buffer productivity at the community level (Tilman & Downing 1994; Chapin *et al.* 1997).

Soil salinity and the frequency of tidal inundation decrease with subtle increases in elevation away from the coast of the Y-K Delta and patterns of plant community zonation are correlated with soil salinity (Tande & Jennings 1986; Kincheloe & Stehn 1991). It has been suggested that vegetation growing along tidally influenced rivers 30 km inland from the coast of the Y-K Delta is salt tolerant (Kincheloe & Stehn 1991). However, salt marsh zonation patterns may not reflect optimal growth conditions for plants inhabiting particular communities and predictions about the response of communities to increased tidal inundation require experimentation (Snow & Vince 1984; Gough & Grace 1999). We hypothesized that soil processes and plant diversity and productivity would be negatively affected by increased tidal disturbance in inland comminutes but that soil processes and vegetation growing in the more coastal environments of this marsh would not be affected by this disturbance. We tested this in the field by flooding three plant communities with tidal waters at different frequencies throughout the 1994 and 1995 growing seasons.

MATERIAL AND METHODS

STUDY AREA

Field experiments were conducted at the Tutakoke River Black Brant (*Branta bernicla nigricans* Lawrence) goose colony (61° 20' N, 165° 38'W) located on the coast of the Bering Sea in southwestern Alaska. The population of Black Brant (hereafter Brant) nesting at the Tutakoke River colony decreased from 7400 to 1100 breeding pairs between 1981 and 1986 (Sedinger *et al.* 1993), but has since increased to an estimated

5600 pairs (R. Michael Anthony unpublished data for 1995). The size of goslings is sensitive to the quality and availability of forage owing, in part, to digestive processing rates (Sedinger & Raveling 1988; Sedinger & Flint 1991). Smaller goslings have lower survival rates, and those that do survive are smaller adults that have decreased recruitment and future fecundity (Sedinger *et al.* 1995). Thus, the potential negative effect of flooding on plant growth and community composition could impact the species of geese that rely the vegetation in this system.

Plant communities in the colony area are < 50 cm above mean tidal range (MTR) (Kincheloe & Stehn 1991). We examined the effect of increased tidal disturbance on the *Carex subspathacea* Wormsk., *C. ramenskii* Kom.-dominated meadows, and slough levee communities. These are the predominant plant communities in the outer coastal zone of the Y-K Delta and they have important life history implications for breeding Brant (Mulder *et al.* 1996, Person *et al.* 1998, Person *et al.* in review). *C. subspathacea* occurs in monospecific swards that constitute the interface between coastal or riparian mudflats, ephemeral pond margins, and within *C. ramenskii*-dominated meadows. Swards of *C. subspathacea* form grazing lawns that are inundated several times diurnally during monthly high tide phases. The *C. ramenskii*-dominated meadow typically occurs along the inland side of the *C. subspathacea* community. These meadows are the most prevalent of the 3 communities contained in the 10 km^2 Tutakoke colony area (Person *et al.*, in review) and are widely distributed throughout the coastal region (Tande & Jennings 1986; Kincheloe & Stehn 1991). Brant typically nest in this community which is *ca.* 3 cm above MTR (Kincheloe & Stehn, 1991). The *C. ramenskii* meadow is

inundated from storm surges of the Bering Sea infrequently (2-3 times decade^{-1}) during the growing season (B.T. Person pers. obs.). Herbivory is patchy in this community, governed ostensibly by snowmelt patterns, proximity to nesting areas and variation in Brant density (Ruess *et al.* 1997, Person *et al.*, in review). Slough levees dissect the Tutakoke landscape and constitute 18 % of the study area (Person *et al.*, in review). This community has the highest species richness of the three communities in the Tutakoke area and is *ca.* 24 cm above MTR (Kincheloe & Stehn 1991; Mulder *et al.* 1996). Geese selectively forage on *Triglochin palustris* L. in this community because of its high concentration of protein relative to cell wall content (Sedinger & Raveling 1988; Mulder & Ruess 1998). Slough levee soils are well drained and have lower soil salinities compared with the other plant communities included in this study.

EXPERIMENTAL DESIGN

We flooded 2 m dia. plots with tidal waters at 3 different frequencies throughout the growing seasons of 1994-95. Treatments included plots flooded 1 (F1), 2 (F2), and 4 (F4) times monthly. A brackish-water treatment (BW: frequency: 2 times per month) was included to distinguish the effects of salt from soil water on edaphic and vegetation parameters. Together with untreated controls (CT), these five treatments were replicated 3 times within each of the 3 plant communities previously described. Replicate plots were spatially separated by a minimum distance of 0.5 km throughout the Tutakoke River colony. Plots were flooded with tidal and brackish-waters using a gasoline-powered pump and 100 m of collapsible hose. Water for saline treatments was obtained either from the Tutakoke River or from an adjoining tidal slough (mean TDS 28.3 ± 0.7 g l^{-1}).

Fresh-water, 250 l per plot, was transported in 200 liter plastic barrels via skiff from a freshwater lake 15 km upriver and mixed with tidal waters for the BW treatments (mean TDS 9.9 ± 1.4 g l^{-1}). Five hundred ± 50 l of water was held on all plots for 1 h during each treatment application by inserting a temporary 3.25 m dia. by 40 cm high Teflon damn into the soil to a depth of 8 ± 3 cm. In both 1994 and 1995 growing seasons plots were flooded: (F4) 16 times, (F2 and BW) 8 times, and (F1) 4 times.

To study the interaction between herbivory and flooding, a 0.5 m diameter permanent exclosure was centered in each plot in addition to small (15 x 15 cm) temporary exclosures distributed throughout the unexclosed portion of each plot (Table 1). Permanent exclosures were established to study the long-term effect of removing grazing pressure on community growth and composition. Short-term exclosures were used to more precisely estimate plant growth in the *C. ramenskii* and *C. subspathacea* communities because grazing pressure on these communities can be high. We estimated net aboveground primary productivity (NAPP) as the difference between biomass in short-term exclosures and unprotected biomass sampled from independent sites approximately 21 d earlier, divided by interval days (McNaughton *et al.* 1996). We did not establish movable exclosures in the slough levee community and measured *NAPP* annually to be the difference between biomass within long-term exclosures and biomass within the unexclosed portion of each plot divided by interval days. Short-term exclosures were not used in this community because geese have little effect on the total standing crop biomass of this community because *T. palustris* comprises a small proportion (< 2%) of the biomass (Mulder *et al.* 1997; Mulder & Ruess 1998).

EDAPHIC MEASUREMENTS

In situ soil redox profiles were measured using platinum electrodes inserted vertically into the soil to a depth of 3 cm. Measurements were made every 30 min for 1 h before, and 6 h post flooding treatment application. Platinum electrodes were acid-etched and calibrated using ZoBell reference solutions (100, 50, 25 % concentrations) prior to measuring each profile (ZoBell 1946). Values were collected using a hand-held voltmeter (Digi-Sense) and transformed to redox potentials by adding the potential of a $Ag^{+}/AgCl^{-}$ reference probe (+ 187 mV). Soil pH was measured using a hand-held pH meter (Digi-Sense) on a slurry of soil by adding 25 mL DDO water to a small soil core that had been dried at 60° C. Soil pH in all communities was similar (mean pH 6.5 ± 0.2; overall *P*-value > 0.6); therefore, we did not adjust redox potentials for soil pH. We averaged redox values measured from 3 probes inserted in each flooded and non-flooded plot. Our level of replication was at the treatment level; being 2 flooded plots and 3 non-flooded plots. We could not samples all blocks and replicates at the same time due to logistic constraints. We assumed that any effects of flooding on redox potential from the week before were ephemeral because some of the non-flooded plots in this analysis had been flooded a week prior to making the redox profiles. This assumption is likely valid (see RESULTS-*EDAPHIC RESPONSES*). Soil water content was measured gravimetrically and is expressed as a percentage of wet weight. Soil- and tide water salinities were measured using a hand-held salinity meter and are presented as total dissolved solutes (TDS). Soil salinity was measured from a small soil core (2 cm diameter x 5 cm depth) taken from each grazed and exclosed portion of each plot at the end of the 1995 growing

season. Wet soils were weighed to the nearest 0.01 g and then dried at 60° C in a field laboratory. Soil TDS was measured by adding 25 mL DDO water to create a soil slurry and values were adjusted for soil mass.

We collected one soil core (5 cm diameter x 10 cm depth) from each exclosed and grazed plot at the end of the experiment to be used for estimating soil carbon and nitrogen mineralization rates. Soil cores were stored in polyethylene bags in a portable cooler and sent to Fairbanks within 36 h. Aboveground biomass was removed 0.25 cm below the soil surface, soil cores were cut in half vertically; half was used for soil incubations and the other for initial mineral nitrogen extraction (see below). Fifty ± 3 g of moist soil was incubated in a 497 mL mason jar in the dark at 12° C for 21 days. Soil respiration was measured every 7 d using a Shimadzu 8A gas chromatograph (Kyoto, Japan). Jar atmosphere was allowed to equilibrate to atmospheric CO_2 after each measurement. Respiration rates ($\mu g\ CO_2$ -C g dwt^{-1} d^{-1}) were calculated as the sum of all 7 d fluxes divided by 21 interval days. Net N mineralization rate (μg N g dwt^{-1} d^{-1}) was calculated as the difference in mineral N ($NH_4^+ + NO_3^-$) extracted with 2N KCl at day 21 and 0 of the incubation.

VEGETATION SAMPLING AND ANALYSIS

Aboveground biomass was estimated 3 times each season with the exception of the slough levee community where, in 1994, biomass was only sampled at the end of the growing season (Table 1). All biomass contained in randomly thrown 100 cm^2 quadrats was clipped to the soil surface, washed in fresh water, sorted to species and standing dead (Hultėn, 1990), and dried at 60 ± 5° C in a field laboratory. Aboveground biomass was

redried and weighed to the nearest 0.001 g upon return from the field. We refer to live standing crop biomass as standing crop biomass hereafter. Forage species were ground in a 20-mesh size Wiley Mill and analyzed for carbon and nitrogen content using a LECO CNS 2000 autoanalyser (Michigan, MI). Species richness is defined as the number of species within each turve sampled within each treatment plot. Species diversity (H′) was estimated using the Shannon-Weiner index where species biomass was used as the proportion of individuals within each sample. Statistical analyses were performed on indexes calculated from standing crop biomass harvested at the end of the 1995 growing season.

STATISTICAL PROCEDURES

We used a nested split-plot design where replicates (blocks) were nested within community. Each block consisted of 5 levels of flooding treatments and each of these plots were split into 3 levels (sub-plot) of grazing treatments (grazed, short-term, and long-term exclosures). Live standing crop biomass was averaged if several turves were sampled in order to avoid pseudoreplication (*for number of turves sampled see* Table 1). We entered: year, time of harvest, flooding treatment, block (replicate), and sub-plots (grazing treatments) as class variables in our ANOVA (PROC GLM) models. *F*-tests for overall treatment variation associated with grazing were tested using the treatment mean squared error (MSE_{graze}) divided by the exclosure x block x treatment interaction MSE. *F*-tests for treatment variation associated with flooding were calculated using the treatment mean squared error (MSE_{flood}) divided by the block x treatment interaction MSE. We removed effects of significant interactions ($P > 0.05$) by limiting analyses to a

single community type. If an overall treatment effect was significant (at alpha < 0.05) we used Tukey's Honest Significant Difference (HSD) multiple comparisons to examine treatment differences. Model assumptions of variance homogeneity were met by transforming data, $\log_{10}(x+1)$, where necessary. Percent soil water data were square root transformed to meet model assumptions.

Redox profiles were analyzed using a repeated measures design (PROC MIXED). Treatment and community were entered as fixed effects. Treatment by time interactions were included to test for an overall treatment effect, followed by linear contrasts between flooded and non-flooded treatments if a significant treatment x time interaction was detected. Within-subject correlation structure was modeled as a compound symmetry (CS) process and we evaluated this model against other correlation structures using Akaike's Information Criterion. All analyses were performed using SAS Institute Inc. (1990) software. All data presented in text represents the mean ± 1 standard error (SE) of non-transformed data.

RESULTS

EDAPHIC RESPONSES

Flooding significantly increased the concentration of dissolved solids in soils of all plant communities (overall treatment effect: $F_{4,8} = 34.5$; $P < 0.0001$). At the end of the 1995 growing season, plots that were flooded weekly (F4) had soils that had doubled, tripled, and increased six fold in TDS concentration when compared to control plots in the *C. subspathacea*, *C. rameneskii* meadow, and slough levee communities, respectively

(Fig. 1). Herbivory exacerbated these effects (overall exclosure effect: $F_{1,24} = 8.9$; $P = 0.007$) in the *C. subspathacea* community where soils in exclosed F4 plots had a mean TDS concentration of 15.0 ± 0.4 in contrast to 27.8 ± 3.1 g TDS gH_2O^{-1} g dwt.$^{-1}$ in grazed soils.

Overall, flooding tended to decrease the redox potential of soils although this effect was not significant in the overall model (linear contrast $F_{1,185} = 3.5$; $P = 0.064$). However, flooding had a strong effect on the redox potential of soils in the slough levee community (linear contrast $F_{1,58} = 20.3$; $P < 0.0001$) (Fig. 2). Although redox potentials were highest in the slough levee community we caution readers that community differences may exist because profiles were not made among communities at the same time of the growing season because of logistical constraints. Thus, community differences may represent seasonal differences in soil redox potentials. Nevertheless, apparent community differences in redox potentials are consistent with the patterns of soil moisture. Percent soil water content was not affected by flooding treatments one week following treatment application ($P > 0.7$). Similarly, protection from herbivores did not affect soil water content ($P > 0.7$). Percent soil water content in control plots was lowest in the slough levee community 58.3 ± 3.5, intermediate in *C. subspathacea* 61.1 ± 5.5 and highest in the *C. ramenskii* meadow 63.4 ± 5.3 (community effect: $F_{2,89} = 6.2$; $P = 0.078$).

Soil respiration rates did not significantly differ among flooding treatments (overall treatment effect: $F_{4,24} = 0.1$; $P > 0.9$) (Table 2). Soils incubated from control plots in the *C. ramenskii* meadow had the highest respiration rates (80.3 ± 3.3 μg CO_2–C

g dwt soil^{-1} d^{-1}) (community effect: $F_{2,89} = 7.6$; $P = 0.0014$). Carbon mineralization of soils from control plots within the *C. subspathacea* (37.7 ± 13.2 μg CO_2 –C g dwt soil^{-1} d^{-1}) and slough levee communities (29.1 ± 8.4 μg CO_2 –C g dwt soil^{-1} d^{-1}) were similar. We did not detect an overall grazing effect on soil respiration rates ($P = 0.14$). However, soils collected from long-term exclosures in the *C. subspathacea* community had higher (80.2 ± 13.8 μg CO_2 g dwt. soil^{-1} d^{-1}) respiration rates than soils from grazed plots when averaged across all treatments (55.6 ± 8.1 μg CO_2 g dwt. soil^{-1} d^{-1}) ($F_{1,4} = 4.79$; $P =$ 0.094).

We detected a small difference in nitrogen mineralization rates between plant communities ($F_{2,89} = 3.24$; $P = 0.049$). Nitrogen mineralization rates were highest in the *C. subspathacea* and slough levee communities (0.23 ± 0.04 and 0.21 ± 0.03 μg N g dwt. soil^{-1} d^{-1}, respectively) and lowest in the *C. ramenskii* meadow (0.13 ± 0.01 μg N g dwt. soil^{-1} d^{-1}). Neither flooding nor grazing had an effect on nitrogen mineralization (*P*-values > 0.7).

ABOVEGROUND RESPONSES

Flooding had no effect on standing crop biomass in the *C. subspathacea* or *C. ramenskii* communities (Fig. 3a,b). However, weekly flooding reduced standing crop biomass in the slough levee community relative to other treatments (Fig. 3c) (treatment effect: $F_{4,28} = 3.77$; $P = 0.024$). Standing dead biomass was greater in both the slough levee and *C. ramenskii* F4 treatment plots when compared to CT plots at the end of the 1995 growing season. Standing dead in F4 and CT treated plots averaged 264 and 152 g dwt. m^{-2} in the slough levee; and 291 and 147 g dwt. m^{-2} in the *C. ramenskii* meadow.

This suggests that the turnover of live biomass was higher in these plots relative to controls. Increased turnover in F4 *C. ramenskii* plots could have precluded the detection of a treatment effect on standing crop biomass. However, we could detect no treatment differences in average *NAPP* in any of the 3 communities in 1995 (overall treatment effect: $F_{4,8} = 1.7$; $P = 0.24$). *NAPP* varied significantly among the 3 communities ($F_{2,119} = 9.7$; $P = 0.0002$). *NAPP* of *C. ramenskii* meadows averaged 2.1 g dwt. m^{-2} d^{-1} and differed from the productivity of *C. subspathacea* swards which averaged 0.47 g dwt. m^{-2} d^{-1}. *NAPP* of the slough levee community did not differ from either community and averaged 1.3 g dwt. m^{-2} d^{-1}.

The negative effect of flooding on the slough levee community resulted from a decline of woody vegetation, predominantly *Salix ovalifolia* Trautv., which averaged 23.7 ± 8.5 g dwt. m^{-2} in F4 plots compared to 138.7 ± 22.1 g dwt. m^{-2} in control plots in 1995. Thus, the proportion of woody to total biomass was decreased in the F4 treatment (0.19) relative to CT plots (0.63). However, the biomass of grass in F4 plots was increased (76.0 ± 18.2 g m^{-2}) when compared to controls (55.8 ± 16.9 g m^{-2}). This suggests that the slough levee community partially compensated from the effects of increased flooding. Neither this trend, nor treatment effects on the slough levee community were apparent by the end of the 1994 growing season.

Flooding did not affect the richness of any community ($P = 0.225$) however, diversity of the slough levee community varied among flooding treatments ($F_{4,59} = 7.1$; $P = 0.026$), tending to be greater at higher soil salinity's (Fig. 4). Changes in community diversity likely represent a shift in the evenness of the slough levee community. We

detected no effect of flooding on the diversity of *C. ramenskii* meadows ($F_{4,59} = 1.4$; $P = 0.25$), and the *C. subspathacea* community is monospecific.

Grazing significantly reduced standing crop biomass in the *C. subspathacea* community (exclosure effect: $F_{2,28} = 179.4$; $P < 0.0001$). Following protection from grazing for two growing seasons, standing crop biomass of *C. subspathacea* did not differ from that of *C. ramenskii*-meadows ($F_{1,28} = 0.53$; $P = 0.47$). We could detect no overall exclosure effect on either the *C. ramenskii* or slough levee communities. However, *T. palustris* biomass within long-term exclosures in the slough levee community averaged 8.1 ± 1.0 g dwt. m^{-2} compared to 3.9 ± 0.5 g dwt. m^{-2} in unprotected plots. It's noteworthy that human trampling around plots in *C. ramenskii*-dominated meadows induced a character state of *C. ramenskii* that made it indiscernible from *C. subspathacea*. This likely reduced grazing pressure on our *C. ramenskii* plots because geese foraged selectively on the surrounding trampled vegetation (B. T. Person *pers. obs.*).

Flooding affected both the nitrogen concentration and carbon to nitrogen ratio (C:N) of *C. ramenskii* and *C. subspathacea* aboveground tissues collected from their respective communities, and grass species collected from within the slough levee community (all treatment *P*-values < 0.04). The nitrogen content of these graminoids was highest when they were growing in saline soils (Table 2). Similarly, C:N ratios were lower in saline treatments. Grazed *C. subspathacea* had increased nitrogen content ($F_{2,8} = 236.4$; $P < 0.0001$) and decreased the C:N ratio ($P < 0.0001$) compared to protected vegetation. This effect reflects differences between vegetation in long-term exclosures and unprotected *C. subspathacea*.

DISCUSSION

The structural and functional characteristics of plant communities that we focused on in this experiment are resistant to short-term effects of changes in tidal inundation. We did not detect a reduction of aboveground biomass until soil salinity was increased by over six times ambient salinity. This response occurred in only one of three communities studied, and resulted largely from a reduction in *S. ovalifolia*, which occurs as a prostrate (5 ± 2 cm high) stoloniferous plant. Iacobella & Jefferies (1991) reported the death of *S. b. brachycarpa* stands in response to increased soil salinity and our results also suggest that the distribution of *Salix spp.* within salt marshes is limited by soil salinity. However, the slough levee community partially compensated for reduced standing biomass through an increase in the biomass of grasses. We suggest that communities containing grasses are resilient to short-term increases in tidal disturbance. Our results are likely representative of changes that would occur following long-term increases in flooding frequency. Acute salinity stress leads to both a rapid reduction in standing biomass of glycophytes and a rapid loss of salt-intolerant species from a community (Jackson & Drew 1984; Wainwright 1984). However, over several growing seasons these effects are often reversed in species that survive acute saline stress, potentially through selection for salt resistant ecotypes (Wainwright 1984; Neumann 1997).

Communities with a diverse assemblage of functional groups are likely to be buffered against disturbances (Tilman & Downing 1994; Chapin *et al.* 1997). We cannot attribute the reduction in woody biomass to salt intolerance versus changes in competitive interactions with grass for nutrients because the scope of our experiment did not

investigate competitive interactions among species within the three communities studied. However, inland marsh communities are structured through competitive interactions (Bertness 1991; Bertness *et al.* 1992; Pennings & Callaway 1992) and competition between woody and grass vegetation for nutrients may have contributed to decreased performance of *S. ovalifolia*, in addition to its apparent salt intolerance. The efficiency of ammonium uptake by plants is inhibited by saline soils (Bradly & Morris 1991; Chambers *et al.* 1998). Graminoid life history traits enable a rapid respond and exploitation to changes in resource availability because of they have higher relative growth rates than do woody plants (Grime 1977). Grasses growing under the most saline treatments likely responded to changes in nutrient competition following the reduction of *S. ovalifolia*. Thus, variation in the life history characteristics among functional groups within the slough levee community stabilized the productivity of this community.

Aboveground tissues of graminoids growing in the most saline treatments had higher nitrogen concentration. Increased leaf nitrogen content can result from differences in plant allometry or from increased cell vacuole concentrations of nitrogen containing molecules used to improve water relations in plants growing in hypersaline soils (Brown & Hellebust 1977; Story & Wyn Jones 1977; Ruess *et al.* 1997). We controlled for differences in allometry by entering standing biomass as a covariate in our ANCOVA model and still detected an increase in N content in these tissues. Ruess *et al.* (1997) attributed increased nitrogen content of *C. ramenskii* tissues grown in saline soils to the accumulation of nitrogen based osmoregulatory molecules. Thus, graminoids likely acclimated to salinity stress through a physiological response.

Biomass turnover may have been greater in *C. ramenskii* meadows that experienced the most saline treatments. For example, there was 112 g more standing dead biomass in slough levee F4 plots when compared to CTL plots; which accounts for the treatment differences in live biomass observed in this community. However, standing dead in *C. ramenskii* F4 plots was 144 g greater than that in CTL plots and standing live biomass did not differ between these 2 treatments (Fig. 2). This suggests that *NAPP* was higher in F4 plots, although our estimates of *NAPP* conflict with this finding. If leaf life-span were shorter in this community we may have underestimated *NAPP* following our sampling interval protocol (Bakker & Loonen 1998). Younger leaf tissues have both higher nitrogen concentrations and water use efficiencies (Kotanen & Jefferies 1987, Oesterheld & McNaughton 1991), and increased leaf turnover suggests that the resilience of this community may be high. Increased leaf turnover offers an additional mechanism through which community productivity is maintained under increased tidal disturbance. This stand level response could lead to an increase in the flow of nutrients to herbivores because young tissues have higher nutritive values, and NAPP may have been higher in the *C. ramenskii* F4 plots than our measurements reflect (Riech *et al.* 1992, Cebrián & Duarte 1994).

Neither soil respiration or nitrogen mineralization were influenced by flooding treatments, suggesting that microbial populations were either resistant to changes in soil salinity and redox potential, or that changes in microbial community structure lead to stabilizing effects on soil carbon and nitrogen processing rates. Higher quality litter has been shown to decompose more rapidly and had we followed aboveground inputs from

the 1995 growing season one would predict that respiration and Nmin rates would have been higher in F4 plots because the nitrogen concentration was increased in aboveground graminoid tissues. Although we detected a decrease in soil redox potential following our flooding treatments (Fig. 2), we believe the aboveground responses occurred as a result of increased soil salinity. Soil salinity in our BW and F1 treatments did not differ (Fig. 1). Linear contrasts between these 2 treatments provided a basis for decoupling the potential effects of soil waterlogging versus increased salinity on above- and belowground processes because soil salinity did not differ between these treatments and soils in BW plots were inundated twice as often than were F1 plots. We detected no differences between these 2 treatments in any parameter we measured. However, when tidal surges occur they inundate soils for up to 6 hours and these soils remain waterlogged for several days following such events (B.T. Person *pers. obs.*). We did not detect differences in either soil water content (one-week following treatment application), or in soil redox potential 3 days after treatments were applied (B.T. Person *unpub. data*). Thus, our examination of the effects of soil waterlogging was conservative because we could not consistently hold water within our dams for more than an hour. The potential effect of soil waterlogging associated with storm surges remains largely untested at the intensity that occurs naturally.

Herbivory decreased the availability of key forage species in the slough levee community and maintained the *C. subspathacea* community as a grazing lawn. Protection from herbivores over two years allowed *T. palustris* biomass to double. *T. palustris* biomass was greater in F4 plots (4.3 ± 0.3 g m^{-2}) than in CTL plots (3.2 ± 0.5 g

m^{-2}) although this effect was not statistically significant. This likely reflects changes in resource competition with neighboring plants rather than a positive effect on growth or recruitment associated with increased soil salinity or waterlogging. Grazing removed over 95% of annual *NAPP* of the *C. subspathacea* community. Protection from herbivores dramatically changed the structure of the *C. subspathacea* community (Fig. 5). *C. subspathacea* within long-term exclosures more closely resembled *C. ramenskii* than unexclosed *C. subspathacea*. Person *et al.* (in review) presents ecological evidence that *C. ramenskii* and *C. subspathacea* are conspecifics whose morphology is controlled by grazing pressure. They describe 'grazed hot-spots' of the *C. ramenskii* community which metastasize into grazing lawns that favor the growth, recruitment, and fecundity of young geese in this population. The reason brant select these forage sites is poorly understood but may be tied to spring snow break-up patterns (Ruess *et al.* 1997). We suggest that hypersalinization of soils may also be a contributing factor influencing food selection. We found elevated leaf nitrogen content of graminoids growing in saline soils and we know geese selectively graze forage high in nitrogen content (Sedinger & Raveling 1988). Because flooding did not have an effect on standing crop biomass of *C. ramenskii*-meadows we suspect that herbivory maybe the primary force that limits its lower zonation. This conclusion is contrary to descriptive studies that concluded these community boundaries were maintained by a salinity gradient (Tande & Jennings 1986; Kincheloe & Stehn 1991). *C. ramenskii*-meadow diversity, aboveground biomass, and *NAPP* were not affected by a three-fold increase in soil salinity.

CONCLUSION

We suggest that both soil processes and aboveground growth of vegetation occurring in the outer coastal zone of the Y-K Delta are resistant to a short-term increase tidal disturbance. Woody vegetation was negatively influenced by a six-fold increase in soil salinity; but not a three-fold increase. Graminoid vegetation compensated for this negative influence and may be critical for the resilience of the slough levee community following increased flooding. Aboveground graminoid tissues from the most saline plots had elevated leaf nitrogen concentrations. *C. ramenskii*-meadows and *C. subspathacea* grazing lawns were not affected by increased tidal disturbance. Finally, herbivory had a strong effect on the structure of the *C. subspathacea* community. The influence of storm driven sedimentation on soil and plant community processes remains to be tested as does a more direct measure of potential effects soil waterlogging on edaphic and aboveground processes. The effects of elevated soil salinity associated with increased storm activity would likely not have a negative impact on the zonation or structure of plant communities in this area.

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LITERATURE CITED

Bakker, C. & Loonen, M.J.J.E., 1998. The influence of goose grazing on the growth of *Poa artica*: overestimation of overcompensation. Oikos, 82, 459-466.

Bellrose, F. C., 1980. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania.

Bertness, M. D., 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* **72**: 125-137.

Bertness, M. D., L. Gough, and S. W. Shumway., 1992b. Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* **73**: 1842-1851.

Bertness, M. D., K. Winkler, and T. Chatkupt., 1992a. Flood tolerance and the distribution of *Iva frutescens* across New England salt marshes. *Oecologia* **91**: 171-178.

Bradley, P. M., and J. L. Morris., 1991. The influence of salinity on the kinetics of $NH4^+$ uptake in *Spartina alterniflora*. *Oecologia* **85**: 375-380.

Brown, L. M. and J. A. Hellebust., 1977. Sorbitol and proline as intracellular osmotic solutes in the green alga *Stichococcus bacillaris*. *Canadian Journal of Botany* **56**:676-679.

Cebrián, J. and C. M. Duarte., 1994. The dependence of herbivory on growth rate in natural plant communities. *Functional Ecology* **8**: 518-525.

Chambers, R. M., T. J. Mozdzer, J. C. Ambrose., 1998. Effects of salinity and sulfide on the distribution of *Phragmites australis* and *Spartina alterniflora* in a tidal saltmarsh. *Aquatic Botany* **62**: 161-169.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. ER. Sala, and D. Tilman., 1997. Biotic control over the functioning of ecosystems. *Science* **277**: 500-504.

Cooch, E. G., D. B. Lank, A. Duzbin, A., R. F. Rockwell, and F. Cooke., 1991. Body size variation in Lesser Snow Geese: seasonal variation in gosling growth rate. Ecology **72**:503-512.

Gough, L. and J. B. Grace., 1998. Effects of flooding, salinity, and herbivory on coastal plant communities, Louisiana, United States. *Oecologia* **117**: 527-535.

Grime J. P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**: 1169-1194.

Hooper, D. U. and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**: 1302-1305.

Hultén, E. 1990. Flora of Alaska and neighboring territories. A manual of the vascular plants. Stanford University Press, Stanford, California.

Iacobelli, A. and R. L. Jefferies. 1991. Inverse salinity gradients in coastal marshes and the death of *Salix*: the effects of grubbing by geese. *Journal of Ecology* **79**:61-73.

Jackson, M. B. and M. C. Drew. 1984. Effects of flooding on growth and metabolism of herbaceous plants. Pages 47-128. *In* T. T. Kozlowski (ed.). Flooding and plant growth. Academic Press, San Diego.

Kincheloe, K. L. and R. L. Stehn., 1991. Vegetation patterns and environmental gradients in coastal meadows on the Yukon-Kuskokwim delta, Alaska. *Canadian Journal of Botany* **69**:1616-1627.

Kotanen, P. and R. L. Jefferies., 1987. The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. *Journal of Ecology*, **75**, 961-975.

Larsson, K. and P. Forslund. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. Journal of Evolutionary Biology **4**:679-686.

McNaughton, S. J., Milchunas, D. G. & Frank, D. A., 1996. How can net primary productivity be measured in grazing ecosystems? *Ecology*, **77**, 974-977.

Mulder, C. P., R. W. Ruess, and J. S. Sedinger., 1996. Effects of environmental manipulations on *Triglochin palustris*: implications for the role of goose herbivory in controlling its distribution. *Journal of Ecology* **84**:267-278.

Mulder, C.P.H. and R. W. Ruess., 1998. Effects of herbivory on arrowgrass: interactions between geese, neighboring plants, and abiotic factors. *Ecological Monographs* **62**:275-293.

Neumann, P., 1997. Salinity resistance and plant growth revisited. *Plant, Cell and Environment*. **20**: 1193-1198.

Nudds, T. D., 1992. Patterns in breeding waterfowl communities. Pages 540-567. *in* B. Batt (ed.). Ecology and management of breeding waterfowl. University of Minnesota press, Minneapolis.

Oesterheld, M. and S. J. McNaughton., 1991. Interactive effect of flooding and grazing on the growth of Serengeti grasses. *Oecologia* **88**: 153-156.

Owen, M., 1980. Wild geese of the world. Batsford Limited, London.

Pennings, S. C. and R. M. Callaway., 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* **73**: 681-690.

Person, B. T., C. A. Babcock, and R. W. Ruess., 1998. Forage variation in brood-rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska. *Journal of Ecology* **86**: 243-259.

Ponnamperuma, F. N., 1984. Effects of flooding on soils. Pages 9-45. *In* T. T. Kozlowski (ed.). Flooding and plant growth. Academic Press, San Diego.

Reich, P. B., M. B. Walters, and D. S. Ellsworth., 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**: 365-392.

Rozema, J. and B. Blom., 1977. Effects of salinity and inundation on the growth of *Agrostis stolonifera* and *Juncus geradii*. *Journal of Ecology* **65**: 213-222.

Ruess, R.W., D. D. Uliassi, C. P. H. Mulder, and B. T. Person., 1997. Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: Implications for geese-ecosystem dynamics in western Alaska. *EcoScience* **4**:170-178.

Sallenger, A. H., 1983. Measurements of debris line elevations and beach profiles following a major storm: northern Bering Sea coast of Alaska. U. S. Geological Survey Open File Report. 83-394.

SAS Institute Inc., 1990. SAS/STAT *User's Guide*, Release 6.04 edition. SAS Institute Inc., Cary, North Carolina.

Sedinger, J. S. and D. G. Raveling., 1988. Foraging behavior of cackling canada goose goslings: implications for the roles of food availability and processing rate. *Oecologia* **75**:119-124.

Sedinger, J. S., C. J. Lensink, D. H. Ward, R. M. Anthony, M. L. Wege, and G. V. Byrd., 1993. Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. *Wildfowl* **44**: 49-59.

Sedinger, J. S., P. L. Flint, and M. S. Lindberg., 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology **76**:2404-2414.

Serreze, M. C., J. A. Maslanik, and J. R. Key., 1997. Atmospheric and sea-ice characteristics of the Arctic ocean in the SHEBA field region in the Beaufort Sea. Special report for National Snow and Ice Data Center, CIRES, University of Colorado, Boulder, CO.

Snow, A. A. and S. W. Vince., 1984. Plant zonation in an Alaskan salt marsh. II. an experimental study of the role of edaphic conditions. *Journal of Ecology* **72**: 669-684.

Srivastava, D. S. and R. L. Jefferies., 1995. Mosaics of vegetation and soil salinity: a consequence of goose foraging in an arctic salt marsh. *Canadian Journal of Botany* **73**:75-83.

Story, R. and R. G. Wyn Jones., 1977. Quaternary ammonium compounds in plants in relation to salt resistance. *Phytochemistry* **16**: 447-453.

Tande, G. F. and T. W. Jennings., 1986. Classification and mapping of tundra near Hazen Bay. Yukon Delta National Wildlife Refuge. Unpublished report, U.S. Fish and Wildlife Service.

Tilman, D. and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* **367**: 363-365.

Wainwright S. J., 1984. Adaptation of plants to flooding with salt water. Pages 295-343. *In* T. T. Kozlowski (ed.). Flooding and plant growth. Academic Press, San Diego.

Walsh, J. E., W. L. Chapman, and T. L. Shy., 1996. Recent decrease of sea level pressure in the central Arctic. *Journal of Climate* **9**: 480-486.

Wilson, D. J., and R. L. Jefferies., 1996. Nitrogen mineralization, plant growth and goose herbivory in an Arctic coastal ecosystem. *Journal of Ecology* **84**: 841-851.

Wise, J. L., A. L. Cominsky, and R. Becker, Jr., 1981. Storm surge climatology and forecasting in Alaska. *Arctic Environmental Information and Data Center, University of Alaska.*

ZoBell, C. E., 1946. Studies on redox potential of marine sediments. *Bulletin of the American Association of Petroleum Geologists* **30**: 477-513.

Table 4.1. Sampling dates (day/month) of aboveground biomass. Number of 10 x 10 cm turves sampled are in parenthesis.

COMMUNITY	*CAREX SUBSPATHACEA*		*CAREX RAMENSKII* -MEADOW		SLOUGH LEVEE	
YEAR	1994	1995	1994	1995	1994	1995
Treatment						
Unexclosed	19/6 (1)	20/6 (1)	20/6 (1)	18/6 (2)	----	21/6 (2)
	13/7 (1)	15/7 (1)	11/7 (2)	12/7 (2)	----	14/7 (2)
	3/8 (1)	1/8 (2)	2/8 (2)	30/7 (2)	31/7 (3)	31/7 (2)
Short-term	----	----	----	----	----	----
exclosure	13/7 (1)	15/7 (1)	11/7 (2)	12/7 (2)	----	----
	3/8 (1)	1/8 (1)	2/8 (2)	30/7 (2)	----	----
Long-term	19/6 (1)	20/6 (1)	20/6 (1)	18/6 (1)	----	21/6 (2)
exclosure	13/7 (1)	15/7 (1)	11/7 (1)	12/7 (1)	----	14/7 (2)
	3/8 (1)	1/8 (1)	2/8 (2)	30/7 (1)	30/7 (3)	31/7 (2)

Table 4.2. Soil respiration rates (μg CO_2-C g_{dwt}^{-1} d^{-1}) from 21 day laboratory incubation of soils sampled from field plots after 2 years of artificial tidal flooding and protection from grazing. Treatments are as follows: flood monthly (F1), flood bi-weekly (F2), brackish water (BW), flood weekly (F4), and control (CT). No differences among flooding treatments ($F_{4,89} > 0.1$; $P = 0.94$), or between soils from grazed and exclosed treatments were found ($F_{1,89} = 1.9$; $P = 0.18$). Data represents the mean ± 1 SE.

Community	*Carex subspathacea*		*Carex ramenskii*		Slough Levee	
	Grazed	Exclosed	Grazed	Exclosed	Grazed	Exclosed
Treatment						
F1	66.2 ± 21	77.3 ± 50	60.5 ± 15	56.2 ± 6	38.1 ± 19	36.0 ± 5
F2	68.7 ± 13	68.7 ± 38	43.5 ± 6	69.7 ± 16	28.6 ± 4	41.1 ± 11
BW	54.3 ± 20	70.6 ± 21	42.6 ± 8	57.7 ± 13	43.1 ± 17	57.2 ± 9
F4	51.1 ± 27	88.7 ± 34	52.0 ± 8	59.1 ± 12	32.2 ± 11	32.4 ± 8
CT	37.7 ± 13	95.8 ± 28	80.3 ± 3	42.5 ± 13	29.1 ± 8	28.9 ± 7

Table 4.3. Nutritional characteristics of key forage species of geese and grass pooled from the slough levee community following 2 years of artificial tidal flooding. Treatments are as follows: flood monthly (F1), flood bi-weekly (F2), brackish water (BW), flood weekly (F4), and control (CT). C:N represents the carbon to nitrogen ratio of foods and is presented as an index the fibre content. Letters shared within columns are not significantly different at alpha > 0.05, Tukey's HSD method.

SPECIES	*Carex ramenskii*		Grass *spp.*		*Carex subspathacea*	
	% N	C:N	% N	C:N	% N	C:N
Treatment						
F1	1.2 ± 0.05 ab	35.9 ± 1.7 ab	1.02 ± 0.06 ab	42.2 ± 2.9 ab	2.6 ± 0.1 ab	14.8 ± 0.7 a
F2	1.3 ± 0.05 b	33.3 ± 1.3 ab	1.01 ± 0.06 ab	42.5 ± 3.0 ab	2.6 ± 0.1 ab	16.9 ± 1.8 a
BW	1.3 ± 0.03 b	33.0 ± 0.8 a	0.87 ± 0.03 b	49.8 ± 2.0 a	2.4 ± 0.1 b	18.9 ± 1.7 a
F4	1.5 ± 0.07 c	29.0 ± 1.4 b	1.23 ± 0.04 a	34.5 ± 1.3 b	3.0 ± 0.2 a	13.7 ± 0.9 b
CT	1.1 ± 0.05 a	38.0 ± 2.0 ab	0.86 ± 0.09 b	49.9 ± 3.4 a	2.6 ± 0.1 ab	16.6 ± 1.1 a

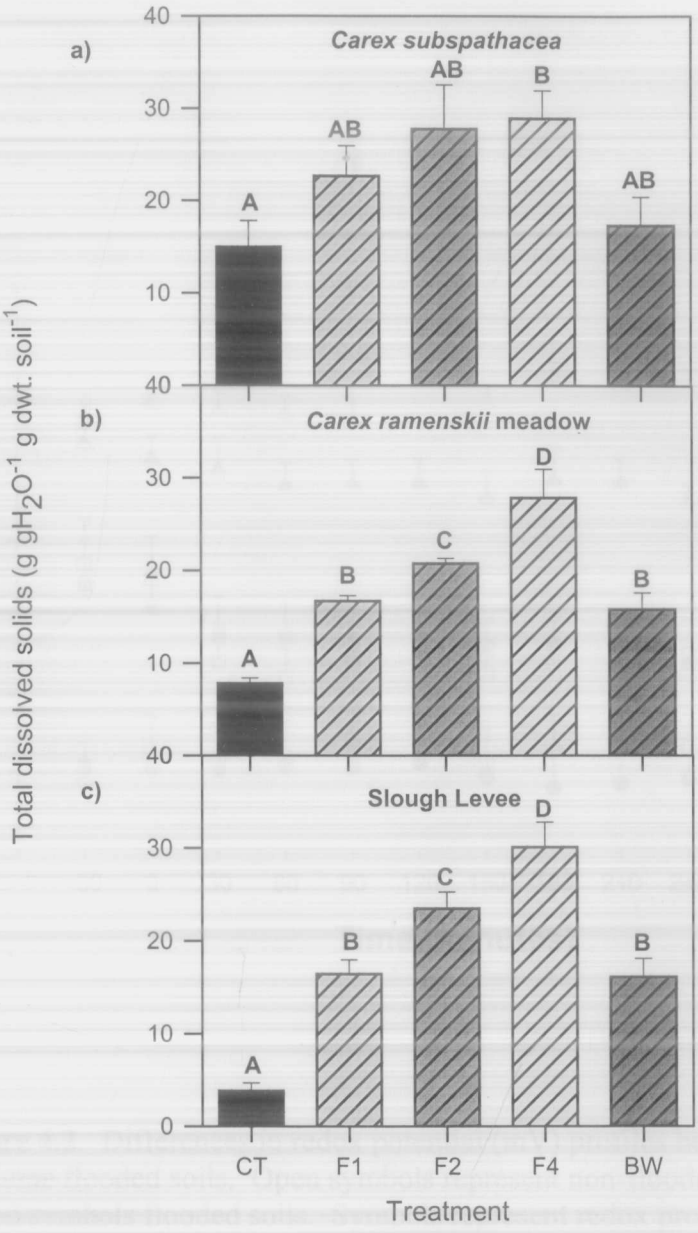

Figure 4.1. The effect of artificial tidal flooding on soil salinity on (**a**) *Carex subspathacea* grazing lawns (**b**) *C. ramenskii*-dominated meadows, and (**c**) a slough levee community. Treatment abbreviations are as follows: control (CT); flood 1 x mo^{-1}(F1); flood 2 x mo^{-1}(F4); flood weekly (F4); and flood 2 x mo^{-1} with brackish waters (BW). Data represents mean ± 1 SE. Soil TDS differed among treatments (overall treatment effect: $F_{4,8} = 34.5$; $P < 0.0001$).

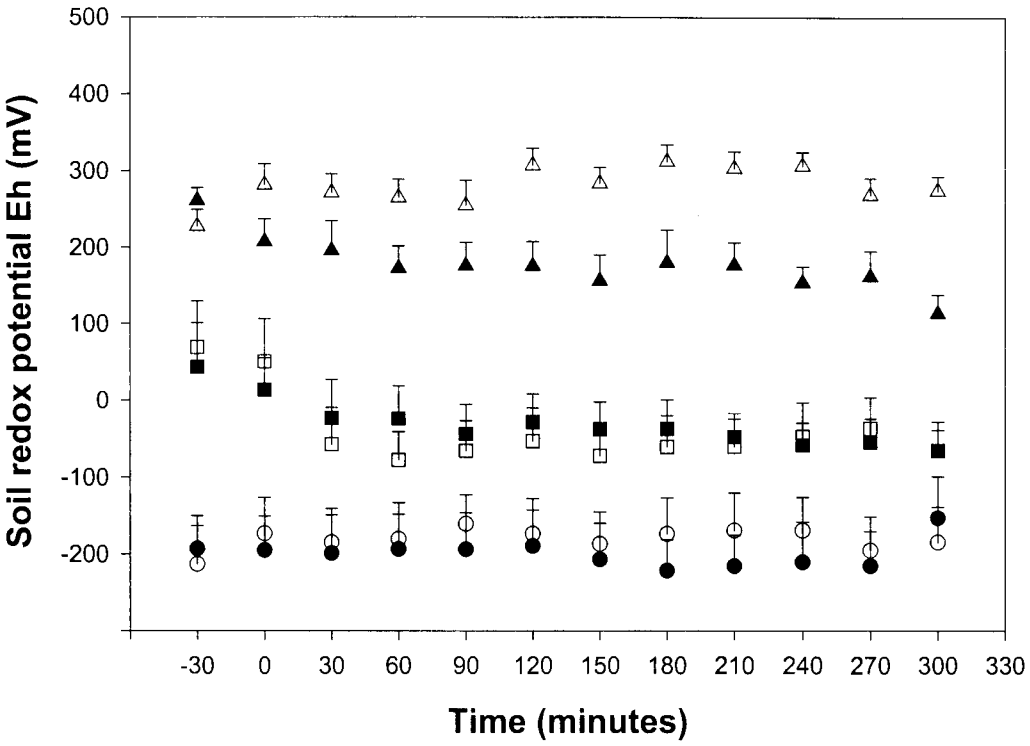

Figure 4.2. Differences in redox potential (mV) profiles between flooded and none flooded soils. Open symbols represent non-flooded soils and closed symbols flooded soils. Symbols represent redox profiles from the: ▲ slough levee community; ■ *C. ramenskii*-dominated meadows; and ● *C. subspathacea* swards.

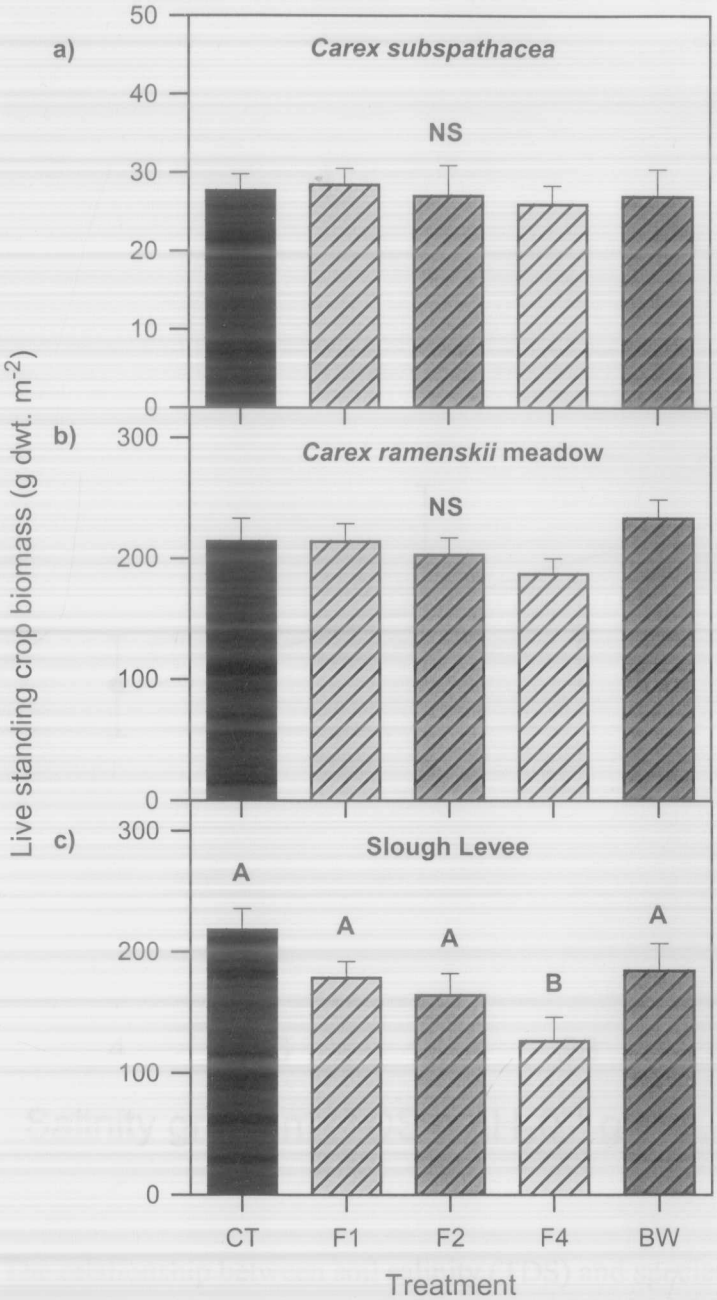

Figure 4.3. Differences in standing crop biomass following 2 growing seasons of treatment application. Biomass represents that harvested at the end of the 1995 growing season. Treatment abbreviations follow those used in Fig. 1a-c. Standing crop biomass differed among treatments within the slough levee community (treatment effect: $F_{4,28} = 3.77$; $P = 0.024$). Letters shared between treatments are not significantly different at alpha = 0.05, Tukey's HSD method of multiple comparisons. Please note axis-scale differences between figures 3 a-c.

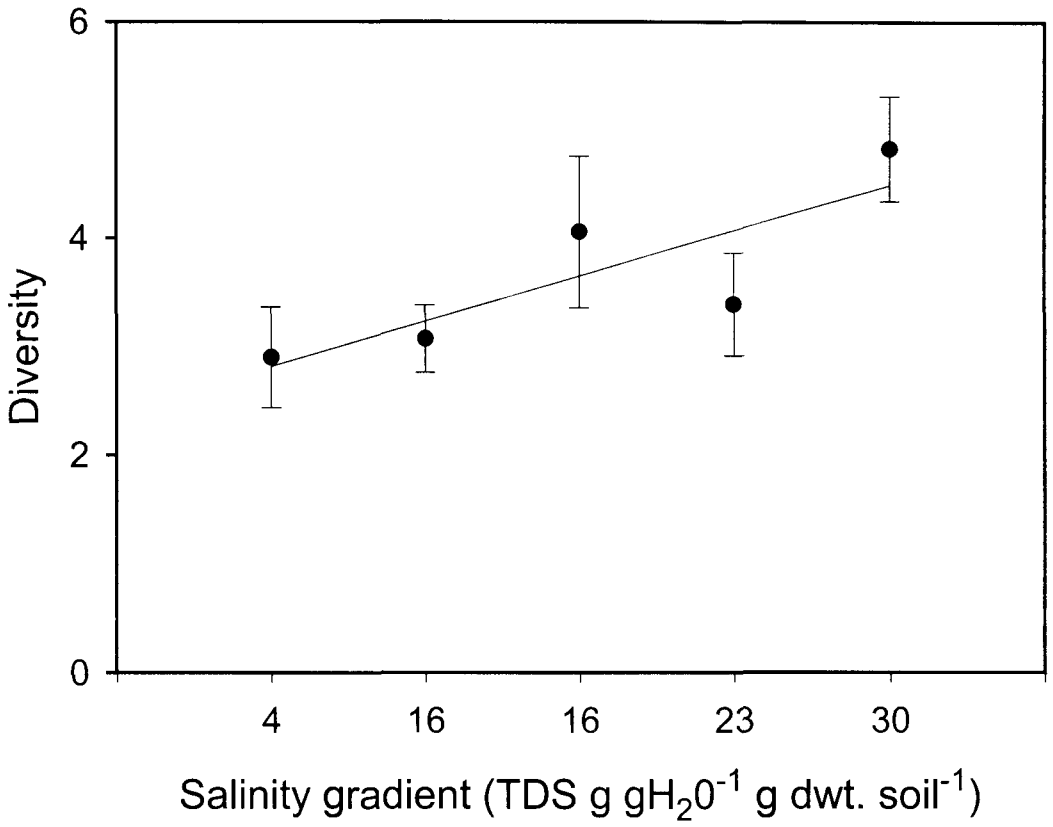

Figure 4.4. The relationship between soil salinity (TDS) and species diversity within the slough levee community.

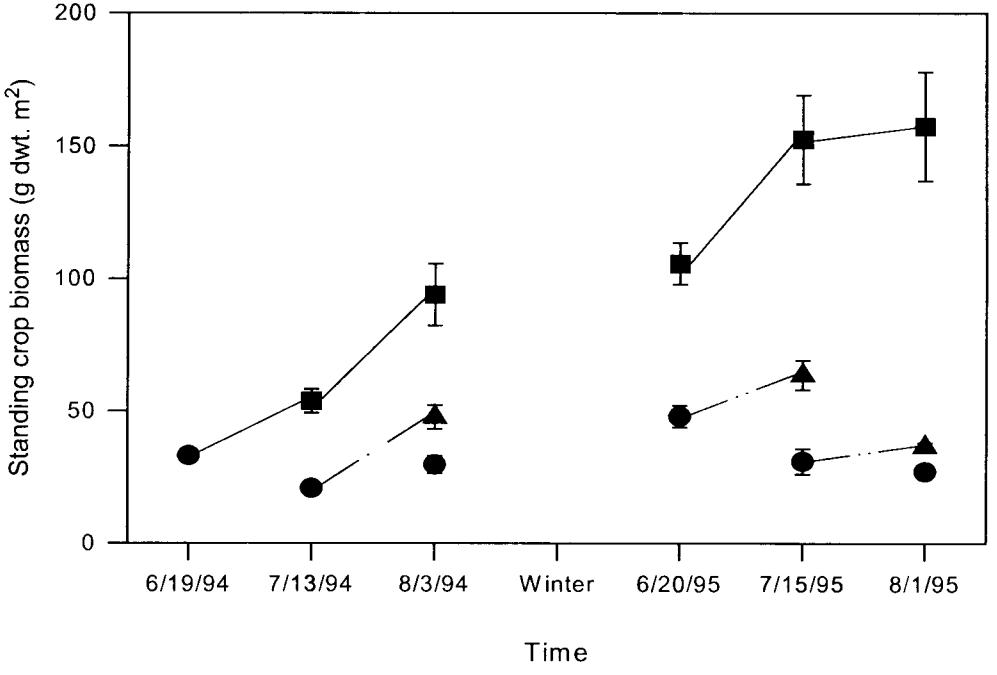

Figure 4.5. Treatment differences in the aboveground biomass of *C. subspathacea* swards over 2 growing seasons of natural goose grazing pressure. Symbols represent: ● continuously grazed swards; ▲ standing biomass following *ca.* 21 days of protection from herbivores; and ■ biomass within long-term exclosures. Data represent mean ± 1 SE.

CONCLUSIONS

Geese breeding in the coastal zone of the Yukon-Kuskokwim Delta are faced with considerable temporal and spatial variation in forage quality and availability, and subtle variation in these characteristics strongly affects survival and fecundity of geese (Owen and Black 1989, Cooch et al. 1993, Sedinger et al. 1995). Black Brant (*Branta bernicla nigricans*) (hereafter Brant) preferentially feed on *Carex subspathacea* despite its low available standing crop biomass and areal extent. Available *C. subspathacea* standing crop nitrogen varied significantly among brood rearing areas to which brant demonstrate within and between year faithfulness (Lindberg and Sedinger 1998, Person et al. 1998). Similarly, the quality of *C. subspathacea* grazing lawns, as indexed by nitrogen concentration, significantly varied among brood rearing areas within the Tutakoke River and Kokechik Bay Brant colonies (Person et al. 1998). *C. subspathacea* nitrogen concentration declined from 4.02 ± 0.14 % to 2.54 ± 0.15 % over the first 42 days of the growing season in the absence of grazing pressure. However, grazing ameliorated seasonal declines in *C. subspathacea* nitrogen content by 129%. Similarly, herbivores were in part responsible for spatial variation in the quality of *C. subspathacea* swards. These feedbacks have profound implications for animal growth given that an 11% seasonal decline in forage quality resulted in captive Cackling Canada goslings (*Branta canadensis minima*) (hereafter Cackling goslings) that were structurally smaller and approximately 100 g lighter.

A discrepancy exists between patterns of landscape use by brant and the nutritional characteristics of forage within these areas. Grazing intensity was higher in areas with low forage quality when compared to other landscapes. This pattern is curious because brant and other geese show some plasticity in their faithfulness to brood rearing sites and dispersal to higher quality brood rearing areas would likely increase gosling fitness during this critical period of gosling growth (Hughes et al. 1994, Lindberg and Sedinger 1998). My data are consistent with Cooch et al. (1993) who reported faithfulness to deteriorating brood sites by Lesser Snow Geese (*Anser c. caerulescens*) even though non-traditional sites of higher quality were available.

However, my data contrast those published on the feedbacks between Lesser Snow Geese and the *C. subspathacea* swards that comprise their brood rearing habitat in the eastern Canadian subarctic (Kerbes et al. 1990). I detected no effect on the net aboveground primary production (NAPP) of *C. subspathacea* despite observing substantial variation of within season grazing pressure whereas Hik and Jefferies (1990) reported a positive feedback between consumers and *C. subspathacea* NAPP. Further, increased populations of Lesser Snow Geese are largely responsible for the demise of brood rearing habitat along the coasts of Hudson and James Bay whereas I report a positive relationship between brant population size, grazing lawn extent, and the mass of goslings reared from the Tutakoke River colony.

Grazing greatly reduced available live standing crop biomass, hereafter SCB, of key forage species without any apparent short- or long-term negative effects on aboveground production. *Triglochin palustris*, and *C. subspathacea* aboveground tissues

had the highest nitrogen concentration of foods measured in this system. Grazing by Brant reduced *T. palustris* SCB by more than 50% over two growing seasons, and Brant consumed over 95% of *C. subspathacea* NAPP within each of two growing seasons for which consumption was measured. Despite this intense grazing pressure, no apparent negative effects on *C. subspathacea* NAPP could be detected within or between two growing seasons. I contrasted the growth response of *C. subspathacea* grazing lawns at four and two landscapes separated by up to 10 km within the Tutakoke River- and Kokechik Bay Brant colonies, respectively. Population dynamics of breeding Brant have differed between the Tutakoke River- and Kokechik Bay Brant colonies over past decades. During the late 1970's and early 1980's grazing pressure was relatively constant at the Kokechik Bay colony but substantially reduced relative to current levels at the Tutakoke River colony (Sedinger et al. 1993). Despite this difference in grazing history between these colonies I found no significant differences in the effects of grazing on NAPP or forage quality of *C. subspathacea* lawns, suggesting that long-term grazing by brant does not have deleterious effects in this ecosystem.

Protecting swards of *C. subspathacea* for two growing seasons changed the structure (*i.e.*, SCB) and aboveground nutritional characteristics such that these swards did not differ from meadows of *C. ramenskii*, a less preferred forage of brant and cackling geese. Addition of grazing pressure to *C. ramenskii* dominated meadows through experimental removal of above ground tissues resulted in swards that brant selected as a grazing lawn. Grazing by brant was responsible for maintaining some of these swards in a state that was morphologically and nutritionally identical to *C.*

subspathacea grazing lawns. In addition, laboratory incubations revealed that carbon mineralization rates of soils from *C. ramenskii* meadows did not differ from soils collected from within long-term exclosures in the *C. subspathacea* community. I surveyed vegetation composition from color aerial videography images collected over the past decade, I found an increase in the areal extent of the *C. subspathacea* community concurrent with a proportional decline in the distribution of *C. ramenskii* meadows. This suggests that grazing controls the zonation of these two communities, and that these reputed species may in fact be grazing morphs of the same species. These sedges were once classified as conspecifics until they were distinguished as separate species based largely on tiller length and floral position in the 1940's (Hultén 1941, 1990). Results from experiment herein suggest that a genetic characterization of these closely related sedges is warranted.

Cackling gosling growth was sensitive to both variation in forage quality and availability. An average 11% decline in the nitrogen content of key foods translated to an approximate 100 g decrease in mass of goslings at 31 days of age. Goslings reared in environments with high forage availability could not fully compensate for seasonal declines in forage quality by increasing intake rates. Since forage quality exerts a stronger effect on gosling growth than does availability, it appears advantageous for geese to nest as early as possible. Forage availability however, is critical for the growth of Cackling goslings. Differences in the availability of foods resulted in similar effects on gosling growth when compared to differences in forage quality. The magnitude of

forage quality and availability effects on gosling development are similar to those observed in wild populations of Cackling geese.

Primary producers and consumers are tightly linked in the coastal zone of the Yukon-Kuskokwim Delta. Consumers affected soil physical and chemical properties, vegetation availability and quality, and plant community zonation. In turn, these effects feed back to influence animal nutrition and growth, survival, fecundity, and goose population dynamics (Sedinger et. al. 1995). I suggest that herbivore-mediated changes in the areal extent of grazing lawns could result in a positive numerical response of the population of Brant breeding at the Tutakoke River colony. Density-dependent conditions have forced Brant to feed on aboveground *C. ramenskii* tissues more than they would under lower population densities. The population of Brant breeding at Tutakoke appears to be at its carrying capacity. However, gosling mass has increased nearly 100 g over the past six years which is inconsistent with this population trend. I attribute the anomalous increase in brant gosling mass to the effect brant grazing has had on the distribution of grazing lawns over the past decade. A positive numeric response of this population is subject to time lags in the differential recruitment and fecundity of cohorts consisting of different size goslings. Similarly, abiotic effects such as storm surges of the Bering Sea during nesting and the effects of predation will dampen herbivore-mediated influences on brood rearing habitat in this system.

Increased tidal flooding on three dominant plant communities in the Tutakoke River colony tended not to influence plant growth or nutrient flow through the food web. I detected a decrease in SCB in the slough levee community when soil salinity was

increased six-fold but not three times ambient soil salinity. This effect was detected only in the slough levee community and resulted from a decrease in biomass of *Salix ovalifolia* aboveground tissues. I could detect no effect of tidal flooding on soil carbon and nitrogen mineralization rates or soil redox potentials in any of the three community types. Aboveground tissues of sedges and grasses growing in the most saline soils had higher nitrogen concentrations relative to unflooded plots, an effect that could plausibly translate into nutritional benefits for geese. Plant communities and soil processes appear to be resistant to the chemical effects of increased tidal inundation in the Tutakoke River landscape. In contrast, increased tidal flooding associated with storm surges resulted in 60% fewer broods produced from the Tutakoke River colony in 1997 when compared to the number of families produced in 1996. This disturbance resulted in a reduction in grazing pressure by Brant, which allowed some long-term plots to revert from grazing lawns, created two years previously, to *C. ramenskii* meadows. Thus, flooding results in strong indirect effects on plant growth and conceivably landscape evolution by removing consumers from this system.

LITERATURE CITED

Abraham, K. F. and R. L. Jefferies. 1997. High goose populations: causes, impacts and implications. Pages 7-72 *in* B. D. J. Batt (ed.). Arctic ecosystems in peril: report of the Arctic goose habitat working group. Arctic Goose Joint Venture SpecialPublication. U. S. Fish and Wildlife Service, Washington D.C. and Canadian Wildlife Service, Ottawa, Ontario.

Bazely, D. R. and R. L. Jefferies. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed marsh. Journal of Ecology, **22**, 693-703.

Cargill, S. M. and R. L. Jefferies. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. Journal of Applied Ecology, **21**, 669-686.

Chapin F. S., D. A. Johnson, and J. D. McKendrick. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: Implications for herbivory. Journal of Ecology 68:189-209.

Cooch, E. G., D. B. Lank, A. Duzbin, A., R. F. Rockwell, and F. Cooke. 1991. Body size variation in Lesser Snow Geese: seasonal variation in gosling growth rate. Ecology **72**:503-512.

Cooch, E. G., R. L. Jefferies, R. F. Rockwell, and F. Cooke. 1993. Environmental change and the cost of phylopatry: an example in the lesser snow geese. Oecologia **93**:128-138.

Coppock D. L., J. K. Detling, J. E. Ellis, M. I. Dyer. 1983b. Plant-herbivore interactions in a North American mixed grass prairie. Effects of black-tailed prairie dogs on

intraseasonal aboveground biomass and nutrient dynamics on plant species diversity. Oecologia **56**:1-9.

Coppock D. L., J. K. Detling, J. E. Ellis, M. I. Dyer. 1983a. Plant-herbivore interactions in a North American mixed grass prairie. Responses of bison to modification of vegetation by prairie dogs. Oecologia **56**:10-15.

Dement, M. W. and P. J. VanSoest. 1985. A nutritional explanation for body-size patterns of ruminant and non ruminant herbivores. American Naturalist **125**:641-672.

DeToit, J. T., J. P. Bryant, and K. Frisby. 1990. Regrowth and palatability of Acacia shoots following pruning by African savanna browsers. Ecology **71**:149-154.

Fox, A.D., H. Gitay, H. Boyd, and C. Tomlinson. 1991. Snow-patch foraging by pink footed geese *Anser brachyrhynchus* in south Iceland. Holarctic Ecology **14**:81-84.

Hik, D. S., Sadual, H. A. and R. L. Jefferies. 1991. Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. Journal of Ecology, **79**, 715-730.

Hobbs, N. T. and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. Journal of Wildlife Management **48**: 551-560.

Hobbs, N. T., D. S. Schimel, C. E. Owensby, and D. S. Ojima. 1991. Fire and grazing in the tallgrass prairie: Contingent effects on nitrogen budgets. Ecology **72**:1374 - 1382.

Hofmann R. R. 1989. Evolutionary steps of ecophisical adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia **78**:443-457.

Hughes J. R., A. Reed, and G. Gauthier. 1994. Space and habitat use by greater snow goose broods on Bylot Island, Northwest Territories. Journal of Wildlife Management 58:536-545.

Hultén, E. 1941. Flora of Alaska and Yukon,1-10. Lunds Universitets. Årsskrift N.F.

Hultén, E. 1990. Flora of Alaska and neighboring territories. A manual of the vascular plants. Stanford University Press, Stanford, California.

Keeling, C. D., J. F. S. Chin, and T. P. Whorf. 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. Nature 382:146-149.

Kerbes, R.H., P. M. Kotanen and R. L. Jefferies. 1990. Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. Journal of Applied Ecology **27**:242-258.

Klein, D. R. 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phonology. Rangifer **3**:123-130.

Kotanen, P. and R. L. Jefferies. 1987. The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. Journal of Ecology, **75**, 961-975.

Larsson, K. and P. Forslund. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. Journal of Evolutionary Biology **4**:679-686.

Lindberg, M. S. and J. S. Sedinger. 1998. Ecological significance of brood-site fidelity in Black Brant: Spatial, annual, and age-related variation. Auk **115**:436-446.

Lindholm, A., G. Gauthier, and A. Desrochers. 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting Greater Snow Geese. Condor **96**:898-908.

McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science **191**:92-94.

McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. BioScience **38**:794-800.

McNaughton, S. J. 1989. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 128:863-886.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798-1800.

Mulder, C.P.H. and R. W. Ruess. 1998. Effects of herbivory on arrowgrass: interactions between geese, neighboring plants, and abiotic factors. Ecological Monographs **62**:275-293.

Nellemann, C. and M. G. Thomsen. 1994. Terrain ruggedness and caribou forage availability during snowmelt on the arctic coastal plain, Alaska. Arctic **47**:361-367.

Oesterheld, M., O. E. Sala, and S. J. McNaughton. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. Nature **356**:234-236.

Owen, M. and J. M. Black. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. Journal of Animal Ecology 58:603-617.

Pastor, J. and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist **139**:690-705.

Person, B. T., C. A. Babcock, and R. W. Ruess. 1998. Forage variation in brood-rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska. Journal of Ecology **86**: 243-259.

Ricklefs, R. E. 1973. Patterns of growth in birds. Growth rate and mode of development. Ibis **115**:177-201.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Academic Press Inc. San Diego, California.

Ruess, R. W., Hik D. H. and R. L. Jefferies. 1989. The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia, **79**, 23-29.

Scott, C. B., R. E. Banner, and F. D. Provenza. 1996. Observations of sheep foraging in familiar and unfamiliar environments: familiarity with the environment influences diet selection. Applied Animal Behaviour Science **49**:165-171.

Sedinger J. S. 1984. Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. Journal of Wildlife Management. **48**:1128-1136.

Sedinger, J.S. & Raveling, D.G. 1986. Timing of nesting by Cackling Geese in relation to the quality and availability of their food plants. Journal of Animal Ecology **55**:1083-1102.

Sedinger, J.S. and D. G. Raveling. 1988. Foraging behavior of cackling canada goose goslings: implications for the roles of food availability and processing rate. Oecologia **75**:119-124.

Sedinger, J. S. and P. F. Flint. 1991. Growth rate is negatively correlated with hatch date in Black Brant. Ecology **72**:496-502.

Sedinger, J. S., Lensink, C. J., Ward, D. H., Anthony, R. M., Wege, M. L. and G. V. Byrd. 1993. Current status and recent dynamics of the Black Brant *Branta bernicla* breeding population. Wildfowl, **44**, 49-59.

Sedinger, J. S., P. L. Flint, and M. S. Lindberg. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology **76**:2404-2414.

Sedinger, J. S. 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. Condor **99**:314-326.

Serreze, M. C., J. A. Maslanik, and J. R. Key., 1997. Atmospheric and sea-ice characteristics of the Arctic ocean in the SHEBA field region in the Beaufort Sea. Special report for National Snow and Ice Data Center, CIRES, University of Colorado, Boulder, CO.

Shipley, LA and D. E. Spalinger. 1995. Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. Oecologia **104**:112-121.

Tardiff, S. E. and J. A. Stanford. 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology **79**: 2219-2228.

van der Wal, R. and R. Drent. 1998. Interactions between hare and brent goose in a salt marsh system: evidence for food competition? Oecologia **117**:227-234.